POPULATION DYNAMICS OF STELLER SEA LIONS, *EUMETOPIAS JUBATUS*,

IN THE EASTERN GULF OF ALASKA

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13 March 2015
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A

DISSERTATION

Presented to the Faculty

of the University of Alaska Fairbanks

in Partial Fulfillment of the Requirements

for the Degree of

Doctor of Philosophy

By

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Fairbanks, Alaska

May 2015

## ABSTRACT

Steller sea lions (*Eumetopias jubatus*) were listed as endangered following a collapse of the western population beginning in the late 1970s. Low juvenile survival and reduced reproductive rates (natality) have been implicated as important factors in the decline. I conducted separate mark-recapture analyses to estimate juvenile survival and natality in an area of the western population where Steller sea lions have begun to show signs of recovery since the early 2000s. I then used these vital-rate estimates in a population matrix to estimate the strength of the recovery and assess which rates pose the greatest threats to recovery. First year survival was estimated at 80% for both males and females, but second-year survival dropped to a low of 40.6% for males and 64.2 % for females that were weaned at age 1. In contrast, survival was greatly improved (88.2%) for males and females that continued to suckle between ages 1 and 2. Cumulative survival to age 4 was double (35.7%) that estimated during the population decline. Natality was also higher in recent years (70%) than during the height of the decline in the 1980s (55%). The mean rate of population growth, based on matrix modeling of vital rates estimated in this study, was 4.1% per year between 2003 and 2013. By projecting these trends into the future, I estimated that the population in the study area may be fully recovered within 14 years, if density independent growth is to be expected in the near future. If density dependent factors come into play, the population will need another 37 years to fully recover. As would be expected from a long-lived, *K*-selected species, population growth rate was most sensitive to variation in adult survival, less sensitive to juvenile survival, and least sensitivity to natality. The findings of this study have important implications for Steller sea lion population management and suggest research priorities should be shifted from an emphasis on natality to an emphasis on survival rates and causes of mortality.

## TABLE OF CONTENTS

## LIST OF FIGURES

Page

## LIST OF TABLES

Page



## LIST OF APPENDICES

Page

## PREFACE

Chiswell Island is located about 56 km south of Seward, Alaska and is home to a small rookery of Steller sea lions (*Eumetopias jubatus*) within the endangered, western distinct population segment. The Alaska SeaLife Center (ASLC) began remote video monitoring of this rookery in 1998 in a collaborative effort between former Alaska Department of Fish & Game biologist, Don Calkins and world-renowned wildlife cinematographer, Daniel Zatz. Since then, researchers at the ASLC have been conducting year-round observations of Steller sea lions in real-time. Up to six cameras on the island, equipped with pan/tilt/zoom functions, are controlled using custom software running on desktop computers at the ASLC. Additional video links to Steller sea lion haulout sites on Grotto Island and near Cape Resurrection were installed in 2001 and 2004, respectively (Figure 3.1). These sites are frequented by Steller sea lions during winter and spring and enhance our knowledge of the biology of this species during these seasons.

Dr. Shannon Atkinson and Don Calkins provided oversight and influenced the direction of the Chiswell Project between 1998 and 2008. I joined the research team in June of 2000 and, along with Pam Parker, have been conducting video observations to better understand Steller sea lion behavior and population dynamics since then. These observations have been supplemented with a variety of field work efforts, including pup sampling and branding, scat collections, and biopsy darting. Over the years, dozens of interns, technicians, and graduate students have assisted in many ways with this research, along with much of the support staff at the ASLC. I could never thank all of them enough in addition to Dr. Alan Springer and the rest of my graduate committee, who have been most helpful and influential in this present work. Yet, in reality, none of this research would have been possible without the foresight, wisdom, and dedication of Shannon, Don, and Pam.

# CHAPTER 1

# GENERAL INTRODUCTION

*General Biology*

The Steller sea lion (*Eumetopias jubatus*), previously known as the northern sea lion, was named in honor of German-born Russian naturalist, Georg Wilhelm Steller, who first described the species in 1741. The scientific name denotes an animal having a mane and broad forehead and is attributed to I. C. D. von Schreber, 1776. The Steller sea lion is the only member of the genus *Eumetopias* and shares the family Otariidae (eared seals) with five additional extant species of sea lions and nine species of fur seals (King 1983; Riedman 1990). The eared seals are grouped together with walruses (family Odobenidae) and true seals (family Phocidae) in the order Pinnipedia.

The Steller sea lion evolved in the North Pacific (Mitchell and Tedford 1973; Repenning 1976) and diverged from the California sea lion (*Zalophus californianus*), its closest relative, between 4.5 and 8 million years ago (Arnason et al. 2006; Phillips et al. 2011). Their current range extends from central California across the northern Pacific Ocean to Russia and Japan in the west. Genetic and morphological studies of Steller sea lions since the mid-1990s have motivated the delineation of eastern and western distinct population segments (DPS) in the United States, divided in Alaska at 144° west longitude (Bickham et al. 1996; O'Corry-Crowe et al. 2006; Phillips et al. 2009). Those studies have further prompted the recognition that the two populations should be considered subspecies and have been designated as *E. j. jubatus* in the western DPS and *E. j. monteriensis* in the eastern DPS (Phillips et al. 2009). The recent divergence among Steller sea lions is believed to have resulted from separation in glacial refugia

during ice sheet advancements 60,000 – 180,000 years ago (Harlin-Cagnato et al. 2006). However, these populations have recently begun intermixing in northern regions of the eastern DPS (Jemison et al. 2013), effectively blurring their genetic distinction near the geographic dividing line.

Steller sea lions are the largest of the otariids and like others in this family, they are sexually dimorphic and polygynous. Males obtain a mean asymptotic length of about 3 m and a weight of 681 kg (Winship et al. 2001), but they can exceed 900 kg (Castellini and Calkins 1993). Mature females grow to 2.4 m and typically weigh between 200 and 300 kg (Winship et al. 2001). The breeding season extends from mid-May to mid-July, when males defend terrestrial territories for the opportunity to mate with several females (Mathisen et al. 1962; Pitcher and Calkins 1981; Thorsteinson and Lensink 1962). Both males and females become reproductively mature at age 3 – 7 years but males do not obtain sufficient size to defend a territory and mate until about age 9 (Pitcher and Calkins 1981; Thorsteinsen and Lensink 1962). Males may live to 15 – 19 years of age in the wild, while females can live into their late 20s (Fiscus 1961; Mathisen et al. 1962; Pitcher and Calkins 1981). Life history studies suggest that reproductive senescence occurs in many pinniped species (Baker and Thompson 2007; Beauplet et al. 2006; Dabin et al. 2004; Melin et al. 2012), including Steller sea lions at more than 20 years of age (Pitcher et al. 1998).

Females that are reproductively active will come into estrus and mate approximately 11 days after giving birth (Gentry 1970; Parker and Maniscalco 2014; Pitcher and Calkins 1981). The fertilized egg undergoes cell division until it reaches the blastocyst stage, then stops dividing during an embryonic diapause that is characteristic among pinnipeds (Atkinson 1997; Pomeroy 2011). Diapause will last approximately 3.5 months in Steller sea lions before active gestation

resumes (Pitcher and Calkins 1981). This transition, mediated by estrogen and progesterone, is likely under environmental influence, such as changes in day length or ocean temperatures (Atkinson 1997; Boyd 1991; Temte and Temte 1993). Active gestation lasts about 8 months over the winter and spring, but in some cases females may resorb a developing fetus for unknown reasons during the early stages of pregnancy (Pitcher and Calkins 1981). However, mid- to late-term abortions may be a more common energy conservation strategy when food is limiting (Gibbens et al. 2010; Pitcher et al. 1998). Full-term pups are born between mid-May and mid-July with a peak around the second week of June, although there is some variation in timing across the range of Steller sea lions (Pitcher et al. 2001).

Mature females give birth to one pup during the breeding season but not necessarily every year (Pitcher and Calkins 1981). Twinning is rare, and some mothers may occasionally nurse a newborn and an offspring from the previous year simultaneously (Maniscalco and Parker 2009; Pitcher and Calkins 1981). While most phocid seals are capital breeders and fast throughout a relatively brief 4 – 60 day lactation period, otariids are income breeders and feed during the lactation period, which may range from 4 months in some species to one or more years in others (Boness and Bowen 1996; Bonner 1984; Oftedal et al. 1987). After parturition, Steller sea lion mothers, like other otariids, typically remain on the rookery for a 4 – 14 day perinatal period, nursing and bonding with their pup before returning to forage at sea (Maniscalco et al. 2006; Milette and Trites 2003; Sandegren 1970). Abbreviated perinatal periods among pinnipeds have been associated with reduced food availability prior to parturition (Boyd et al. 1991; Hood and Ono 1997; Ono et al. 1987; Stewart and Yochem 1991).

Attendance patterns after the perinatal period may also vary depending on food availability (Heath et al. 1991; Lunn et al. 1993; Ono et al. 1987) and seasonality (Maniscalco et

al. 2006; Melin et al. 2000; Merrick and Loughlin 1997). Steller sea lion females in Alaska generally have brief (< 1 day) foraging trips during early summer, which begin increasing in duration by late summer to a mean length of 2 or more days during fall and winter (Maniscalco et al. 2006; Milette and Trites 2003; Trites and Porter 2002). Females and their offspring often move seasonally from rookeries to haulout locations that provide protection from violent winter storms (Loughlin et al. 2003; Sease and York 2003). Between foraging trips, nursing bouts continue at the haulouts until around April – June when offspring are weaned (Raum-Suryan et al. 2004; Trites et al. 2006). While the timing of weaning is relatively consistent in late spring to early summer each year, the age at which offspring are weaned can range from 1 to 4 years (Pitcher and Calkins 1981; Trites et al. 2006).

Many overwintering adult female Steller sea lions are both pregnant and lactating at the same time, in addition to taking extended foraging trips and dealing with freezing temperatures in many places (Pitcher and Calkins 1981). Their energetic demands should be at a peak during this time of year. To meet those energetic demands, prey resources must be abundant and available, and according to some captive studies (e.g., du Dot et al. 2008; Kumagai et al. 2006), of good nutritional quality. Adults should be able to compensate for low fat prey items by consuming more prey, but that might not be possible for juveniles (Rosen 2009). Nevertheless, during overwintering periods when food may be limiting, an adult female that is lactating and pregnant has 3 primary life history choices: 1) she may continue the pregnancy and nurse her offspring at the risk of her own future survival, 2) she may wean her offspring early to save energy for the current pregnancy and survival, or 3) she may abort the pregnancy and continue to nurse the current offspring. These choices are not necessarily mutually exclusive under extreme conditions. Although lactation is considered to be the most energetically expensive of these

options (Gittleman and Thompson 1988; Oftedal et al. 1987), fetal abortions appear to be the more conventional choice for pinnipeds in this situation (Gibbens et al. 2010; Pitcher et al. 1998; Testa 1987). That choice reflects a common strategy among long-lived mammals in which adult survival and juvenile survival are favored over reproduction (Hamel et al. 2010). This has important consequences for the population dynamics of any species (Bell 1980), but other factors, such as disease, predation, and anthropogenic interactions, can also have large impacts on populations.

*Population Dynamics*

Data from archaeological middens found along the Gulf of Alaska and eastern Aleutian Islands, including stable isotope signatures found in prey items and human remains, suggest that Steller sea lions experienced several major population fluctuations over the past 4,500 years (Maschner et al. 2014; Misarti et al. 2009). In relatively recent history, populations were at a low in the late 1800s to early 1900s, then peaked again at nearly 300,000 individuals in the 1970s (Loughlin et al. 1984; Maschner et al. 2014; Trites and Larkin 1996). By 1989, the Steller sea lion population again declined by 65%, and the species was listed as threatened under the U.S. Endangered Species Act in 1990 (Loughlin et al. 1992). Declines were most drastic in the western DPS, continuing through the 1990s (Sease et al. 2001), and prompted the 1997 up-listing to endangered status for Steller sea lions in this region. Similar declines during this period were also noted along the coast of Russia (Burkanov and Loughlin 2005), but not in the eastern DPS, where the population has been stable or increasing (Calkins et al. 1999; Pitcher et al. 2007).

Many causes for the late 20$^{th}$ century decline of Steller sea lions have been hypothesized and studied. Disease, pollutants, subsistence harvest, and emigration are not believed to have

been major factors in the decline, but direct and indirect effects of fisheries, ecosystem changes, and predation by killer whales (*Orcinus orca*) have received more attention (Atkinson et al. 2008; Loughlin 1998; National Research Council 2003). An estimated 20,000 Steller sea lions were killed by direct interactions with the fishing industry (primarily shooting and net entanglements) between 1968 and 1985 and most were females (Fritz et al. 1995; Loughlin and Nelson 1986). Indirect mortality may have resulted due to intense competition between humans and Steller sea lions for the same fishes, mainly walleye pollock (*Gadus chalcogrammus*) and Atka mackerel (*Pleurogrammus monopterygius*). This potential competition may have been particularly acute during the height of the population decline, when groundfish removals peaked at around 2 million tons per year in the 1970s and 1980s (Alverson 1992; Fritz et al. 1995). Those interactions prompted the imposition of catch restrictions with time and location, and quotas for many fisheries have been implemented in the vicinity of major Steller sea lion rookeries (Fritz and Ferrero 1998). The fishing restrictions likely helped to mitigate the decline as population trends in the Gulf of Alaska and Aleutian Islands stabilized after their enactment (Hennen 2006).

The idea that environmental changes may have contributed to the Steller sea lion decline is centered on warming ocean temperatures following the 1976 meteorological regime shift over the North Pacific Ocean as indexed by the Pacific Decadal Oscillation (PDO, Mantua et al. 1997). The PDO was believed to influence a shift in the forage fish community from a dominance of small, lipid-rich fishes, such as herring (*Clupea pallasii*), capelin (*Mallotus villosus*), and sand lance (*Ammodytes hexapterus*) to a greater abundance of relatively lipid-poor fishes, such as pollock and Pacific cod (*Gadus macrocephalus*) between the 1970s and 1990s (Alverson 1992; Anderson and Piatt 1999; Trites and Donnelly 2003). With those ecosystem

changes, it was thought that Steller sea lions were feeding more on lipid-poor foods during the period of decline compared with earlier years and were not able to consume sufficient nutrition to meet their metabolic demands (Rosen and Trites 2000; Trites and Donnelly 2003). Those findings were backed by observations of a slight reduction in body size of adult females in the 1980s compared with the 1970s (Calkins et al. 1998), and a variety of captive studies showed negative impacts on physiological and immune function during times when Steller sea lions were fed a lipid-poor diet (e.g., du Dot et al. 2008, 2009; Rosen and Trites 2000). However, many of those findings have been disputed from both ecological and physiological perspectives, including the facts that cod and pollock have always been a significant portion of Steller sea lion diets, and they often gain weight by consuming such foods (Atkinson et al. 2008; Calkins et al. 2013; Fritz and Hinckley 2005). In addition, there has been no empirical evidence of a decline in the abundance of herring, sand lance, or other high lipid fishes, other than capelin in a portion of the WPDS range, at a time when it could explain the Steller sea lion collapse (Fritz and Hinckley 2005; Springer et al. 2008).

Another widely debated hypothesis for the Steller sea lion population decline is based on increased predation by killer whales between the 1970s and 1990s (Springer et al. 2003). The premise behind that hypothesis is that mammal eating (transient) killer whales once fed to a great extent on a variety of large baleen and sperm whales (*Physeter macrocephalus*). Industrial whaling operations, which peaked after World War II, removed as much as 90% of the great whale biomass. This prompted killer whales to begin feeding more on smaller but readily available prey in a sequential manner, such as harbor seals (*Phoca vitulina*), Steller sea lions, fur seals (*Callorhinus ursinus*), and sea otters (*Enhydra lutris*; Estes et al. 2009; Springer et al. 2003). This hypothesis is appealing in that it logically follows what we know about prey

switching and foraging theory in many animals (Emlen 1966; Stephens and Krebs 1986) and explains enormous population declines of a variety of pinnipeds during this time period, which can be influenced by minor changes in killer whale diets (Williams et al. 2004). Nevertheless, this hypothesis has been heavily criticized; for example, there is little evidence that killer whales ever fed much on great whales, the pinniped population collapses were not exactly sequential and not consistent with great whale depletions, and that other theories better explain the population collapses (DeMaster et al. 2006; Mizroch and Rice 2006; Trites et al. 2007).

Despite considerable monetary expenditure and a multitude of scientific studies over the past 25 years, there is still no general consensus of what caused the Steller sea lion population decline. However, some modeling studies have found good evidence to implicate a variety of factors in the decline (e.g., Guinette et al. 2006; Pascual and Adkison 1994; Wolf and Mangel 2008). Regardless of the ultimate cause(s), changes in vital rates are the proximate cause of population fluctuations. Age-specific survival and natality (female reproductive rate) are primary factors that affect population change. A 10 – 20% drop in juvenile survival, coupled with slight drops in natality and adult survival, was determined to have caused the observed Steller sea lion decline during the 1980s (York 1994). Later modeling studies based on counts of adults and juveniles on rookeries and haulouts suggested that juvenile survivorship had returned to normal levels by the 1990s, but that natality continued to plummet (Holmes and York 2003; Holmes et al. 2007). Attempting to estimate natality for Steller sea lions in this way, however, is fraught with problems and uncertainties (Maniscalco et al. 2010). Long-term studies based on observations of marked individuals provide the best means to assess population dynamics, especially vital rates (Clutton-Brock and Sheldon 2010).

The purpose of this study was to provide new estimates of juvenile survival and natality based on long-term observations of marked individual Steller sea lions within the endangered, western DPS. Their populations have begun to recover in much, but not all, of this region since about 2000 (Fritz et al. 2013). Understanding the mechanisms and sustainability of this recovery requires detailed long-term monitoring. The year-round observations that span more than a decade during this study have provided a large dataset for accurate vital rate estimations. In Chapter 2, I estimate juvenile survival in Steller sea lions with respect to how birth weight, sex, and extended maternal care influence survival over the first four years of life. Chapter 3 focuses on natality rates over a 10-year period and tests for long-term trends and interannual variation in natality. Chapter 3 further examines if census count data, based on ratios of pups and mature females, can be used as a proxy to estimate natality. Finally, in Chapter 4, I applied the vital rates estimated in Chapters 2 and 3 to a population matrix model to determine if these rates are consistent with observed population trends on both local and broader spatial scales. These trends are extended into the future using a prospective analysis to determine which vital rate(s) has the most influence on population trends.

Several pinniped populations have recovered from critically low levels throughout recorded history (Gerber and Hilborn 2001), and Steller sea lions appear to be doing the same. This study not only describes the vital rates that represent this rapidly recovering population, but also examines some factors that can have an influence on vital rates, such as the quality and extent of maternal care. The findings of this study indicate that natality, adult survival, and juvenile survival in the study area are good. Furthermore, negative changes in survival would pose a greater threat to population recovery than natality. Therefore, I suggest that Steller sea

lion population management priorities should be shifted from an emphasis on natality to an emphasis on survival rates and causes of mortality.

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# CHAPTER 2

## THE EFFECTS OF BIRTH WEIGHT AND MATERNAL CARE ON SURVIVAL OF JUVENILE STELLER SEA LIONS (*EUMETOPIAS JUBATUS*)[1]


### ABSTRACT

Steller sea lions were listed as endangered following a collapse of the western distinct population beginning in the late 1970s. Low juvenile survival has been implicated as a factor in the decline. I conducted a multistate mark-recapture analysis to estimate juvenile survival in an area of the western population where sea lions are showing signs of recovery. Survival for males and females was 80% between 3 weeks and 1 year of age. Approximately 20% of juveniles continued to be nursed by their mothers between ages 1 and 2 and 10% between ages 2 and 3. Survival for juveniles that suckled beyond 1 year was 88.2% and 89.9% to ages 2 and 3, respectively. In contrast, survival for individuals weaned by age 1 was 40.6% for males and 64.2% for females between ages 1 and 2. Birth mass positively influenced survival for juveniles weaned at age 1 but had little effect on individuals continuing to suckle. Cumulative survival to age 4 was double that estimated during the population decline in this region. Evidence suggests that western Steller sea lions utilize a somewhat different maternal strategy than those in the eastern distinct population. Western adult females generally invest more in their pups during the first year but wean offspring by age 1 more often. This results in better survival to age 1, but greater mortality between ages 1 and 3 compared to the eastern population. Different maternal


[1] Maniscalco JM (2014) The effects of birth weight and maternal care on survival of juvenile Steller sea lions (*Eumetopias jubatus*). PLoS ONE 9(5):e96328, May 7, 2014.

strategies may reflect density dependent pressures of populations at opposite levels of abundance.

## INTRODUCTION

Juvenile survival is an important life history variable affecting population growth and can be greatly influenced by environmental variation in large iteroparous mammals [1,2]. Environmental factors affect maternal body condition, health, and pregnancy status which, in turn, can affect reproductive rates and juvenile survival [1,3,4]. The quality and extent of maternal care among mammals can be measured by attentiveness to offspring needs in the form of nurturing or nursing, and subsequent survival of those offspring. The stage at which offspring are weaned and become independent has limited flexibility among most mammals and may depend on a complex interplay of parent and offspring needs with respect to available resources among other things [3-5]. Variation in the duration of maternal care and nursing reaches an extreme among otariid pinnipeds (fur seals and sea lions) where it can vary between 8 months and 4 years for certain species [6,7]. Yet, there have been no direct measures of the effect that continued maternal care has on survival rates among juvenile pinnipeds.

Steller sea lions (*Eumetopias jubatus*) are the largest of the otariids and likely have the largest variation in the duration of lactational dependence [6,8]. Females of this species become reproductively mature at 3 to 7 years of age and give birth to one pup per year but not necessarily every year [6]. Twinning is extremely rare and adult females may occasionally nurse offspring of different ages simultaneously [9].

Since the 1970s, Steller sea lions in the western distinct population segment (WDPS; [10,11]) of the North Pacific Ocean declined by over 80% [12] and are currently listed as

endangered under the Endangered Species Act of the United States. Most of the decline occurred during a catastrophic collapse spanning about 15 years between the late 1970s and early 1990s. Much research during the past two decades has been dedicated to understanding potential causal factors such as nutritional limitation due to interaction with economically important fisheries [13,14] or climate change [15], and predation by killer whales (*Orcinus orca*; [16]). Early survival estimates for WDPS sea lions were based on age composition counts and life history tables [17,18] and indicated that juvenile survival was reduced during the height of the population decline in the Gulf of Alaska during the 1980s compared to the 1970s. A subsequent estimate of juvenile survivorship during the period from 1987 to 1991, based on mark-recapture analysis of individuals from approximately 3 weeks of age, suggested good survival to age 1 (80%) but much lower survival for ages 1 – 2 and 2 – 3 (61% per age group; [19]). Both studies implicated low juvenile survival as a contributor to the population decline.

Steller sea lion populations and pup production have generally increased since 2001 between the eastern Aleutian Islands and Gulf of Alaska regions of the WDPS with the most strongly positive trends observed in the Gulf of Alaska [20]. This may be due in part to high natality rates of adult females in this region [21]. Improved juvenile survival may also be aiding the observed recovery. A recent estimate based on actual detection of mortalities in a small sample of juveniles between 2005 and 2011 suggested that survivorship had recovered somewhat since the 1980s to 64% for animals 1 – 2 years and 83% from 2 to 3 years [22]. Similarly, mark-recapture estimates of annual Steller sea lion survival in the eastern distinct population segment (EDPS) in southeastern Alaska range from 65% to 97% for males and females aged 1 to 4 years [23]. The EDPS has also been increasing over at least the past few decades [24,25]. It is

naturally important to understand what factors might be affecting these changes in juvenile survival.

The purpose of this study was to provide an updated estimate of pup and juvenile survival from age 3 weeks to 4 years based on mark-recapture data from the WDPS that can be compared to similar work during the WDPS decline [19] and current estimates in the EDPS [23]. Results presented in the current work cannot be clearly compared to the earliest estimates of survival based on juvenile proportions and life history models [18] because of different assumptions made between that study and this one. I also estimated the effect that birth mass and multiple years of maternal nursing had on juvenile survival along with proportions weaned at ages 2 and 3 using a multistate mark-recapture approach [26,27]. Birth mass has often been found to have an effect on future survival in pinnipeds and terrestrial mammals [1,23,28,29]. However, among mammals that exhibit large variations in maternal dependence, how long a mother nurses her offspring may have an even greater effect on future survival [7,30,31]. These and other covariates were tested among Steller sea lions in this study to gain a better understanding of how female life history choices can affect juvenile survival in this endangered species.

## MATERIALS AND METHODS

### *Ethics Statement*

This research was conducted in accordance with Alaska SeaLife Center Institutional Animal Care and Use Committee Protocol No. R10-03-01 and National Marine Fisheries Service Permit No. 14324 for research on endangered Steller sea lions. The Chiswell Island group is part of the U.S. Fish and Wildlife Service National Maritime National Wildlife Refuge.

Research was conducted on Refuge lands under right-of-way Permit No. M-344-AM and Special Use Permit No. 74500-10-001 and earlier versions.

*Study Site and Field Methods*

This study was centered on Steller sea lions from the Chiswell Island rookery in the eastern Gulf of Alaska, part of the endangered WDPS (Figure 2.1). Sea lions at this rookery and the surrounding area have been well-studied since 1999, primarily through the use of a remote video system [21,32]. Pups were captured at the rookery on one day in each of the years 2005, 2007, 2008, and 2010 near the end of the pupping season (June 30 – July 3). Body mass was determined by weighing pups to the nearest 0.1 kg in a tared hoop net with a hanging electronic scale (FWC series 7, FlexWeigh, Santa Rosa, CA). While anesthetized in sternal recumbence on a flat board, pups were sexed, measured and permanently marked by hot-iron branding as described by Merrick et al. [33].

Age at capture in previous studies such as this has been assumed to be about 3 weeks based on time from peak birthing periods [19,23,34]. In this study, most adult females were individually recognizable by natural markings, brands, or tags, and monitored for timing of birth and attendance patterns [32]. Therefore, it was possible to determine the exact age of marked pups in almost all cases when they reunited with their mothers whose time of parturition was known to within ± 4 hrs. This assumes that mothers reunited with their own pups and not others, and was considered reasonable given that otariids form strong mother-pup bonds from a very young age [35-37].

Resighting efforts were conducted during systematic scan sampling as described by Altmann [38] using the remote video system based on Chiswell Island and neighboring haulouts

in the surrounding area [21,32]. These local efforts were supplemented with observations from small boats and tour vessels. Additional resightings throughout Alaska came from dedicated annual efforts by the National Marine Fisheries Service and Alaska Department of Fish & Game. Only sightings that could be verified with a photograph were used in this analysis. Behavior of each of the resighted animals was recorded with special attention to nursing activity of the mother. The annual observation window extended from 20 June through 31 October to utilize data from a broad range of sources and dedicated efforts. Observation effort also was consistent between years with number of days of effort varying <5% from all sources across years.

It was not always possible to determine if a juvenile was still suckling and with its mother beyond 1 year of age, especially when only one or few observations of the animal were recorded. Kendall et al. [39] provide a robust design method for dealing with state uncertainty such as this but that method requires a large increase in parameters being estimated. The increased parameterization combined with the relatively short duration (<7 years) of this study plus the inclusion of an individual covariate (birth mass) resulted in poor performance of many models using that approach. Therefore, a standard multistate approach was used, but with ancillary information on the location and status of the mothers, state uncertainty was greatly reduced. For example, if a juvenile was observed without its mother in any location, we would cross-check our database for the status of the mother at that time. If the mother was attending to a newborn pup on the rookery without the elder sibling, then it would be confirmation that the previously marked juvenile had been weaned. This left only 2 juveniles of unknown status and with their removal from the dataset, allowed the use of a standard multistate modeling approach rather than robust design multistate modeling.

*Data Analysis*

Data were analyzed in Program MARK under a multistate design [40,41] using the logit link function to estimate survival (S), sighting probabilities (p), and state transitions probabilities ($\psi$) for juveniles up to age 4. Two different states were designated as suckling (s) and independent or weaned (w). Transitions between states ($\psi^{SS}$ and $\psi^{SW}$) were assumed to be Markovian such that state observed at time *i* was dependent only on the state observed at time *i*-1. Transition from independence back to suckling ($\psi^{WS}$) is rarely observed in the wild for this species (ASLC unpublished data), so was constrained to 0. Sex was included as a grouping variable and birth mass (range: 13.2 – 32.4 kg) as an individual covariate for each pup. Birth mass was estimated from linear regressions based on mass at capture versus age for each sex and cohort. The regression residuals for each pup were added to the y-intercepts to obtain the mass estimates. Estimates of birth mass by this method are considered to be of "high quality" [42].

Multinomial models were compared with an information-theoretic approach to provide a relative strength of evidence for alternative models [43,44]. This technique uses Akaike's Information Criteria (AIC; [45]) with an additional correction for small sample bias (AICc; [46]) to determine the best fitting model(s). The fully parameterized time-dependent model was first tested for goodness of fit (GOF) using program U-Care [47].

Other than the state transition constraint mentioned above, 2 additional constraints were placed on all fitted models, with the exception of the fully parameterized time-dependent model. First, survival was constrained to be equal for juveniles transitioning to independence and for those continuing to suckle between ages 0 and 1 because weaning typically occurs between April and mid-June in this species [8], which is outside our late-June to October observation period. In this manner, state transition was assumed to have occurred late in the non-observation period and

survival was dependent only on previous state. Second, probability of sighting a suckling juvenile ($p^s$) was constrained to 1 for all ages and both sexes because this value was found to be very close to 1 in preliminary analysis and had confidence intervals exceeding 1, which can cause models of this type to perform poorly [27]. Further constraints to the models were placed with regard to biological relevance in the search for the most parsimonious model(s) that provide the most information with the fewest parameters. For example, survival of suckling juveniles was constrained to be equal between the sexes for some models tested. If those models express much smaller AICc values (more parsimonious) than other models in which survival was allowed to vary between sexes, then it can be said that survival is not different between males and females that are suckling. In this manner, a variety of constraints were placed on survival, sighting probabilities, and state transitions to be tested for their effect on model fit.

Parameter estimates were obtained from averaging all models that fit the data using the modern principals of multimodel inference [44,48]. Estimates of survival are of apparent survival because actual deaths could not be differentiated from permanent emigration. Combined survival estimates for all individuals at each age were determined from proportions estimated in each state and sex category with error calculated using the Delta Method of R. Dorfman [49] with variance-covariance matrices provided from Program MARK. Calculation of the proportion of juveniles that were suckling at different ages was performed using equation 2 in Nichols et al. [50] with corresponding estimates of error.

## RESULTS

A total of 199 pups over the 4 cohorts were captured, weighed, and observed at least once with their mothers whose time of parturition was known. Pups in this study ranged from 5 – 38

days old at time of capture and were close to 3 weeks on average (19.8 ± 0.51 d). All regressions for mass-at-age of the neonate pups were highly significant ($P < 0.001$) for each sex and cohort, providing reasonable estimations of mass at birth (Figure 2.2). Mass at birth ranged from 13.2 to 28.2 kg for females (n = 89) and 14.0 to 31.4 kg for males (n = 108). Two pups could not be positively identified with their mother and were assigned the mean estimated birth mass based on the regressions for their sex and birth year. This method provides accurate representation of relatively small proportions (1% in this case) of missing data [51]. Resightings of juveniles were concentrated within a few hundred km of their birth location at Chiswell Island. However, a few individuals ranged as far west as the Alaskan Peninsula and as far east as Glacier Bay in the EDPS, ca. 800 km in either direction. Movement of these and many other marked Steller sea lions in Alaska were examined in another study [52].

Based on GOF tests of the full model, there was an insignificant degree of overdispersion with regard to the effect of past encounter history and with regard to capture probability for individuals known to be alive ($\hat{c} = 1.27$, $P = 0.298$). Therefore, no overdispersion estimate was applied to AICc values.

In addition to the fully time dependent model, 35 additional models were fitted with various logical constraints on all parameters examined (Table 2.1). Effects of time and cohort on survival, sighting probability, and state transition were not well supported by the data. Models with sighting probabilities for independent juveniles ($p^{w}$) varying between ages 1 – 4 and with sex differences were better supported than those with equality between the sexes. As noted in the methods, sighting probabilities for suckling juveniles ($p^{s}$) were close to 1, and therefore constrained to 1, and were not different between the sexes. Sighting probabilities ranged from

about 32% to 100% for independent male and female juveniles and generally increased with age (Table 2.2).

Transition probabilities from suckling to weaning ($\psi^{SS}$ and $\psi^{SW}$) that were constrained to be equal between the sexes had better strength of evidence than those varying between the sexes indicating no difference in age at weaning for males and females. Birth mass was not favored as a contributor to age at weaning, first appearing in the 12$^{th}$ ranked model with a ΔAICc of 4.692 (Table 2.1).

As anticipated, survival probabilities (S) were best represented by differences between juveniles that were suckling in year $i - 1$ and those that were weaned at $i - 1$. The best fitting model with survival set to be equal between those 2 groups ranked 18$^{th}$ with a ΔAICc of 8.327 and a likelihood of <0.02 (Table 2.1). All of the best fitting models expressed some effect of sex on survival for independent juveniles ($S^W$) but not for those continuing to suckle ($S^S$), indicating that males and females that continued to suckle beyond 1 year of age benefitted equally. Mass was also included in most of the best fitting models as an important contributor to survival for weaned juveniles but generally not favored for an effect on survival for juveniles still suckling (Table 2.1).

Survival to age 1 was estimated at 80.1% for all juveniles but dropped to a low of 40.5% for weaned ($S^W$) males between ages 1 and 2 (Figure 2.3). Survival estimates also generally increased with age, especially for independent females and for males and females that continued to suckle. Estimated birth mass was positively correlated with survival for independent males and females between 1 and 2 years of age (Figure 2.4a and 2.4c). Not surprisingly, this effect was weaker as the juveniles aged (Figures 2.4b and 2.4d). Combined survival estimates for suckling and non-suckling males and females were similar to those during the period of the

decline to ages 1 and 2, but were greatly improved during the recent period for juveniles to ages 3 and 4 (Figure 2.5). Cumulative survival to age 4, when many females become reproductively mature [6], was 35.7 ± 8.2% (SE).

Most juveniles were weaned by one year of age, but 16.9 ± 2.2% of males and 22.6 ± 1.8% of females were estimated to continue suckling between ages 1 and 2. Between ages 2 and 3, these proportions declined to 11.2 ± 2.7% of males and 8.2 ± 2.3% of females. Only one individual female and no males were observed to nurse beyond age 3. That particular female nursed through age 4 and gave birth for the first time to her own pup at age 5.

## DISCUSSION

### *Survival Comparisons Past and Present, East and West*

Determining factors that affect juvenile survival is a fundamental problem for population ecologists. By comparing and contrasting the behaviors of conspecifics with differing population trends, we may gain some insight into mechanisms of variation in juvenile survival. Such mechanisms are ultimately the result of environmental influence but are often tempered through the quality and extent of maternal care [1,3]. Western and eastern Steller sea lions provide an interesting study in contrast of the possible effects of differing maternal strategies as discussed below.

Survival from 3 weeks of age to 1 year was very high (nearly 80%) among WPDS sea lions in this study. This estimate is the same as it was during the period of the decline in this region [19] and generally better than in the EDPS where survival to 1 year was <60% at the largest and oldest rookeries and between 62% and 76% at 2 smaller, newer rookeries [23]. Even between ages 1 and 2, the combined estimates in this study for both suckling and non-suckling

males and females were similar to estimates during the population decline in this region at about 57.5%, being diminished by the poor survival probability of weaned males in this age group. The improvement in survival over estimates during the decline in the WDPS seems to begin after age 2 with a jump to 89% in this study compared to 58% from earlier estimates [19]. Survival from age 2 and older was more similar between this study and current estimates from the EDPS [23] where populations have been increasing [24,25]. Overall, cumulative survival to age 4 in this study was double (35.7%) the estimate during the decline in the WPDS (17.9%; [19], providing evidence that more females are recruiting into the breeding population in recent years. Food availability has been implicated as a primary contributor of survival to recruitment age among some pinnipeds [53,54]. For Steller sea lions, a variety of factors including food availability and killer whale predation may affect recruitment [12,55] and some of these are discussed in more detail below.

*The Effect of Mass*

Among pinnipeds, survival has been correlated with pup mass and several maternal factors including parturition date, pupping location, and maternal age, experience and mass [28,53,56-60]. Notwithstanding differences between sexes, it is common among mammals for smaller individuals to have reduced chances of survival, especially during periods of greater resource competition or reduced food availability [28,61-63]. In this study, birth mass was positively correlated with survival to 2 and 3 years of age among females and males that were weaned by age 1, but was unimportant for juveniles that continued to suckle past age 1. The same positive effect of mass at 2 – 4 weeks of age on survival through at least the first few years of life was found for EDPS Steller sea lions with the correlation diminishing for older animals

[23]. However, pups that are smaller or grow more slowly may be able to compensate for their disadvantage by continuing to suckle later in life [7,64]. Indeed, this study shows that mass was not an important contributor to survival for juveniles that continued to suckle beyond their first year of life.

*The Effect of Extended Maternal Care*

Post-partum maternal care likely plays a greater role than birth mass in the future survival of offspring and this is believed to be true for phocids but more so for otariids with extended lactation periods [31,65,66]. Furthermore, large otariids such as the Steller sea lion give birth to relatively small young compared to smaller pinnipeds [67] making post-partum maternal care especially important in this species. Females that have difficulty transferring sufficient energy to their offspring risk mortality of the offspring or their own reduced fitness [29,31,68,69]. Yet, pinnipeds that are able to adjust their lactation length are better adapted to changing environmental conditions [7] and this sort of adjustment can help offspring to reach a critical mass needed for weaning. Threshold mass and growth rates are believed to be the primary factors influencing the timing of weaning among large mammals [30,64,67]. It was not possible to measure weaning mass among Steller sea lions in this study, and birth mass was not found to contribute to the timing of weaning. Nevertheless, some interesting differences become apparent when comparing maternal investment and survival studies on a broader scale.

Mothers of pups in the Gulf of Alaska (WDPS) have longer perinatal periods and shorter foraging trips than mothers in the EDPS [32,70], suggesting better maternal care early in life for WDPS pups. Furthermore, young pups have been found to be larger [71] and grow faster in both mass and size within the WDPS compared to the EDPS [72]. Although specific correlations

have not been tested, it is reasonable to suggest that better maternal care early in life translates into better survival for WDPS sea lions through their first year compared to EDPS sea lions as explained herein. This study shows that continued maternal care has a positive influence on survival beyond 1 year of age. After their first year, offspring of EDPS mothers may be more likely to continue suckling, with as much as 70% observed doing so [8]. In contrast, only about 20% of WDPS juveniles suckle past age 1 with a corresponding large decrease in survival for individuals that were weaned. EDPS animals have better overall survival between ages 1 and 3 [23], which might be attributed to proportionally more juveniles continuing to suckle at older ages.

As pups are born heavier and grow faster in the WDPS, we can generalize that adult female sea lions in this region invest more in their offspring early in life and are able to wean them at an earlier age, whereas EDPS females provide less care early on but continue care for a longer period. This latter strategy is typical among otariids during times, and at locations, of low food availability [7], which may be the case for EDPS Steller sea lions. The population in the east is at the highest level seen in the past century [24] and likely subject to more intraspecific competition for resources compared to WDPS sea lions that are far below historical numbers. There is also some evidence that average age at weaning was increasing in the west between 1960 and 1983 in conjunction with a theorized reduction in food availability [73]. I suggest here that weaning age in the west has returned to base levels that are indicative of good food availability and that turnaround may have begun in the late 1980s – early 1990s as represented by good first-year survival during that time period [19]. However, some interannual variation in age at weaning may still persist [74], although it was not observed in this study. These comparisons between WDPS and EDPS Steller sea lions suggest that plasticity in the duration of

maternal care is an important density dependent mechanism for populations at low and high levels of abundance respectively.

*Sex Differences in Survival*

Differences in survival between juvenile male and female sea lions also provide an interesting study in contrasts. Juvenile males had lower survival probabilities than females to age 4 in this study. This was also the case for Steller sea lions in the expanding EDPS [23], but not during the WDPS decline [19]. Among pinnipeds, lower juvenile survival of males compared to females has also been observed in subantarctic fur seals (*Arctocephalus tropicalis*; [62]) and grey seals (*Halichoerus grypus*; [75]), but lacking in New Zealand sea lions (*Phocartos hookeri*; [76]), California sea lions (*Zalophus californianus*; [77]), and southern elephant seals (*Mirounga leonina*; [78]).

Hastings et al. [23] make several plausible arguments as to why male survival can be lower than female survival in Steller sea lions, including greater growth and maintenance requirements among males [79], a theory expounded by Clutton-Brock et al. [80]. The cost of physiological maintenance requirements in juvenile male Steller sea lions can be exacerbated by increased energy expenditure in more frequent, prolonged, and intense bouts of play behavior compared to females [81]. However, it should then follow that we might expect a further reduction in survival for males compared to females during times when high-quality food is less abundant [80] as it may have been during the period of the WDPS decline [15,82,83]. Yet, survival was differentially lower for females during the period of the decline compared to present day, whereas male survival to age 2 was actually better during the period of the decline than it has been in recent years ([19] vis-à-vis this study). Similar trends were found in subantarctic fur

seals with females having a greater reduction in survival from years of good or average environmental productivity to years of poor productivity compared to males [62]. In these cases, the larger mass of males may provide some buffering against reduced resource availability as exemplified by the greater annual fluctuations in mass that males cope with compared to females [79]. Alternatively, males may be more persistent in suckling during times of reduced food availability [84]. This might explain their relatively better survival during the period of the decline and why proportionally more males than females suckle at older ages in the EDPS [8] compared to the WDPS (this study).

Explanations for sex differences in juvenile Steller sea lion survival during periods of good prey availability may include risks associated with greater travel distances by males [23,85], and 'incautious' behavior of males leading to entanglements [86]. Energy expenditure associated with greater travel distances outside the normal home-range of subantarctic fur seals was implicated as a contributor to the higher mortality found in juvenile males [62]. Incautious behavior and broader travel ranges could also make males more susceptible to predation. Juvenile mortality in Steller sea lions has been strongly linked to predation in the eastern Gulf of Alaska with a greater proportion of males taken compared to females in a recent study, although the difference was not significant within the small sample [22]. Continued maternal care may temper imprudent behavior of juvenile males by providing increased vigilance or protection against predators. A similar effect of maternal vigilance on juvenile survival was also found in a predatory land mammal, the cheetah (*Acinonyx jubatus*; [87]).

Juvenile survival is an important element in the dynamics of populations and minor changes could have large impacts on pinniped populations [88]. High juvenile survival, coupled with recent high natality [21], may be important contributors to the recovery of the Steller sea

lion population in the Gulf of Alaska following the catastrophic collapse in abundance throughout the Gulf of Alaska, Aleutian Islands, and Bering Sea. Survival likelihoods, and perhaps the primary causes of mortality, can differ between the sexes depending on interdecadal changes in food availability or predation pressure. The idea that Steller sea lions in much of the WDPS are doing better from a nutritional perspective than those in the EDPS in recent years is not new [12,89]. However, this study offers new insight into how maternal care might affect the survival of different age classes of young sea lions and how adjustments can be made to ensure long-term success of the population. The results presented here should encourage further work into how variations in maternal care may provide some resilience to drastic population changes among long-lived mammals.

**ACKNOWLEDGMENTS**

The remote video team for this study was expertly led by Pamela Parker and data collection accomplished by many hard-working technicians and interns at the ASLC including Carly Miller, Juliana Kim, Emily Teate, and many others. Thanks also to Lauri Jemison (ADF&G) and Rod Towell (NMFS) for brand resightings outside of our study area. James Estes, Tom Gelatt, and an anonymous reviewer provided comments on an earlier draft of the manuscript. Alan Springer, Milo Adkison, Lara Horstmann, Chuck Frost, and Tuula Hollmen offered critiques and commentaries, and much helpful advice on this material. Discussions with Lorrie Rea helped development of ideas about age at weaning.

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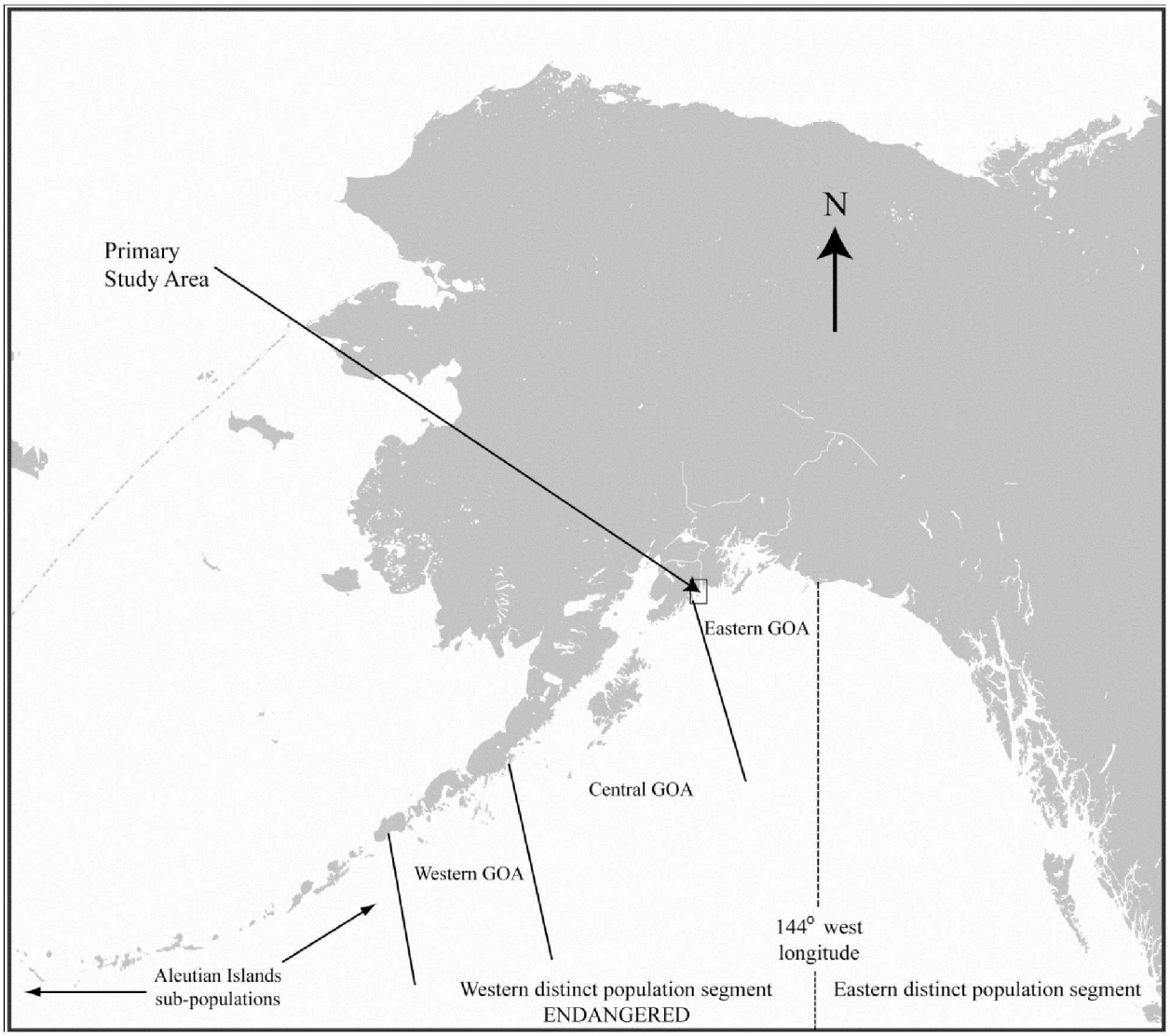


Figure 2.1 – Map of Alaska showing the delineation between the western (endangered) and eastern distinct population segments of Steller sea lions and the primary area of study for this research in the eastern Gulf of Alaska (GOA).

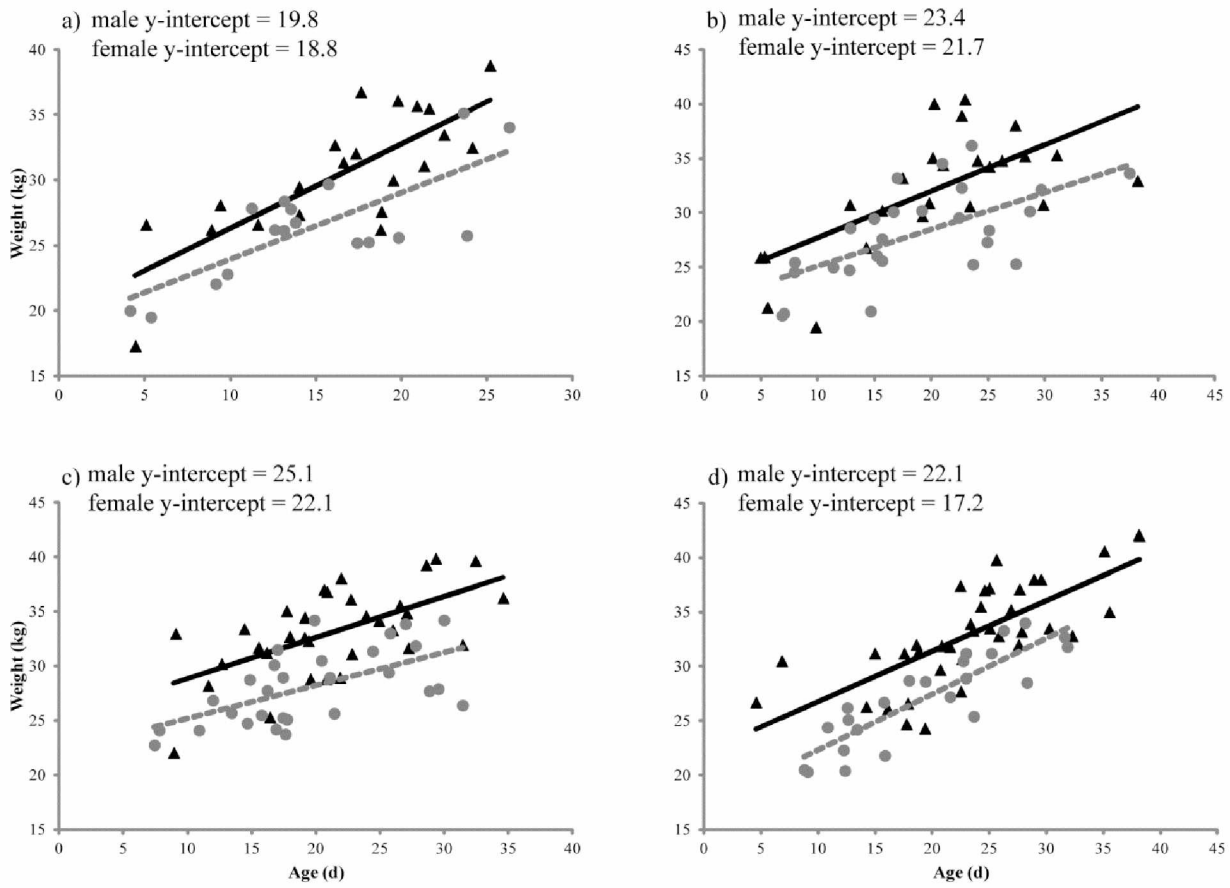


Figure 2.2 – Regressions of mass on age for males (▲) and females (●) from a) 2005, b) 2007, c) 2008, and d) 2010. Residuals for each individual were subtracted from the y-intercept by sex and year to obtain birth mass estimates. All regressions were highly significant ($P < 0.001$).

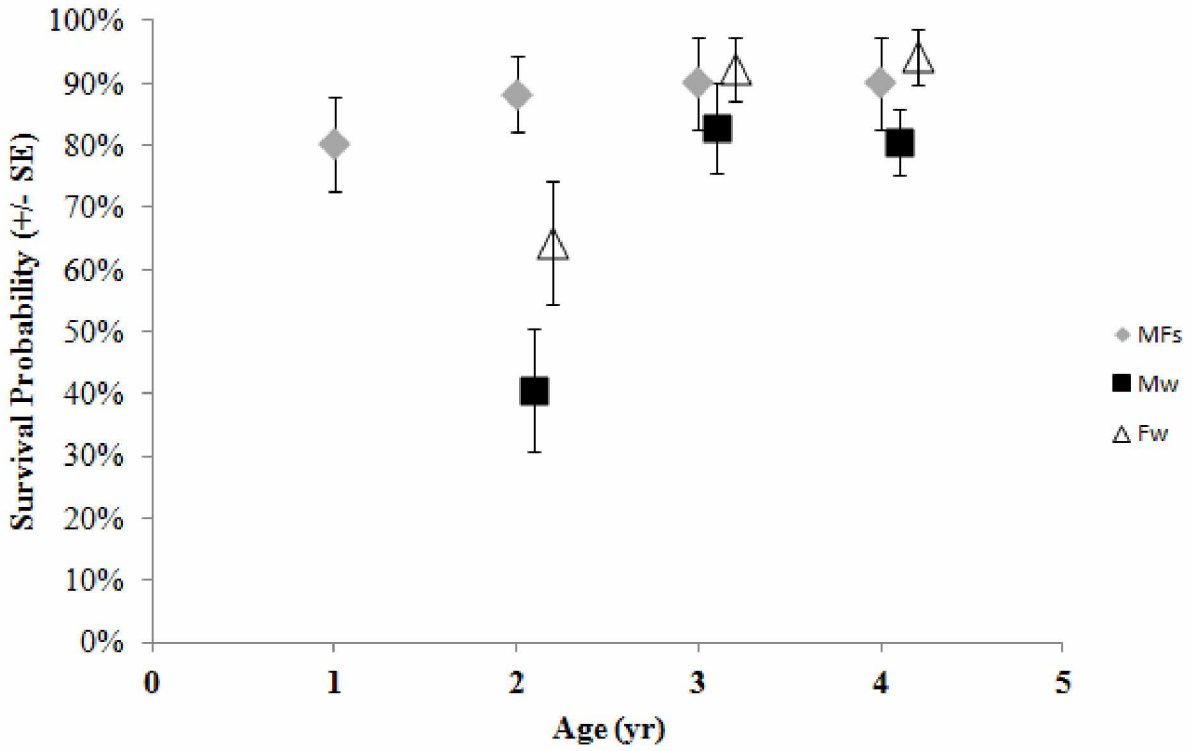


Figure 2.3 – Model-averaged survival estimates (± SE) of Steller sea lions to ages 1 – 4 for suckling males and females (MFs), weaned males (Mw) and weaned females (Fw).

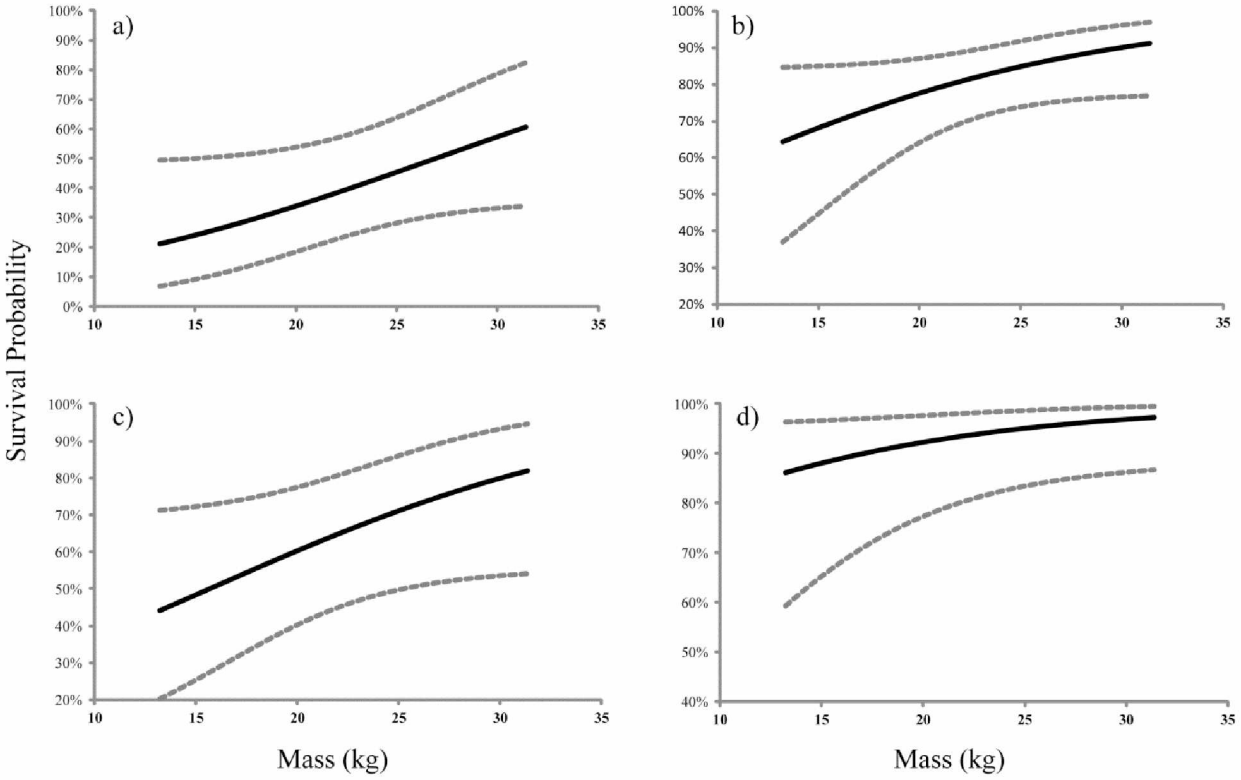


Figure 2.4 – The effect of birth mass on survival for independent juveniles: a) males to age 2, b) males to age 3, c) females to age 2, and d) females to age 3. Note different y-axis scales.

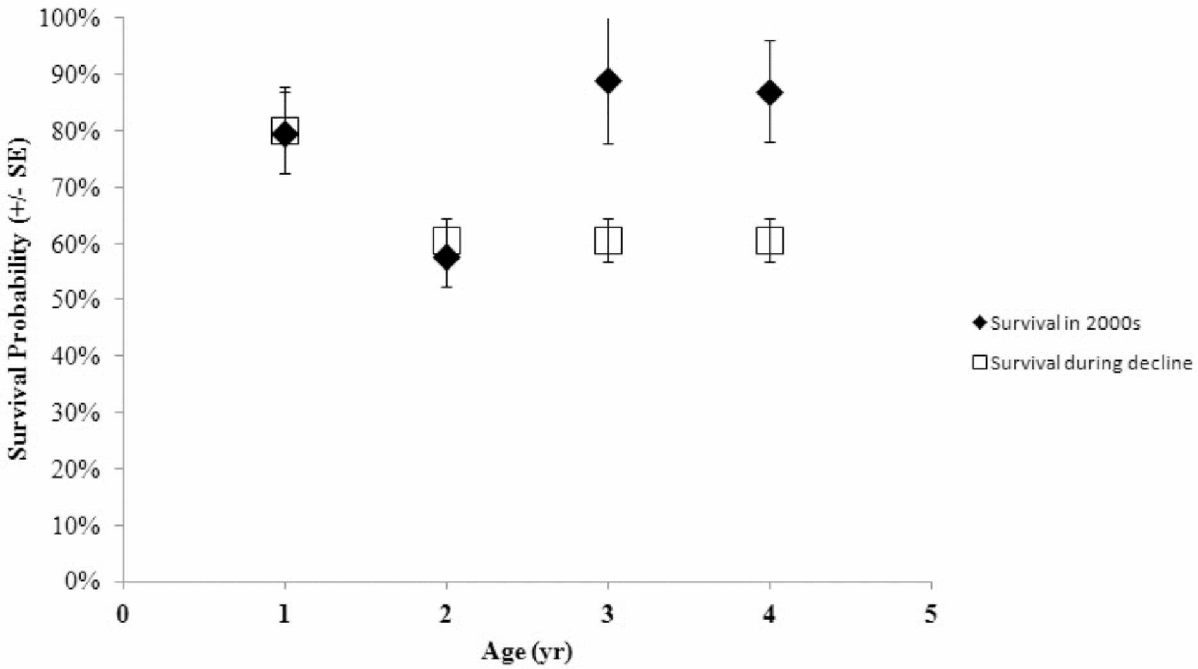


Figure 2.5 – Survival probabilities for male and female juveniles at age during the period of the decline (open squares; [19]) and during the 2000s (closed diamonds; this study).

Table 2.1 – Parameter structure for multistate models fit to the data in this study. Ages represent separation of years with older ages than listed being grouped as similar. $S^s$ and $S^W$ represent survival of those suckling and those weaned in year $i - 1$, respectively. Sighting probability structure for individuals that were weaned ($p^W$) is represented by p and those that were suckling ($p^s$) constrained to 1. State transition from suckling to independence is represented by ψ.

| Model | AICc | ΔAICc | AICc weight | Model Likelihood | No. Parm |
|---|---|---|---|---|---|
| $S^s$(age1,2)$S^W$(mass+sex*age2,3) p(sex*age1-4) ψ(age1-3) | 970.757 | 0.000 | 0.223 | 1.000 | 20 |
| $S^s$(age1,2)$S^W$(mass+sex*age2,3) p(sex*age1-4) ψ(age1-5) | 971.376 | 0.619 | 0.163 | 0.734 | 22 |
| $S^s$(age1,2)$S^W$(sex*age2,3) p(sex*age1-4) ψ(age1-3) | 971.892 | 1.135 | 0.126 | 0.567 | 19 |
| $S^s$(mass+age1,2)$S^w$(mass+sex*age2,3) p(sex*age1-4) ψ(age1-5) | 972.353 | 1.595 | 0.100 | 0.450 | 23 |
| $S^s$(age1,2)$S^W$(sex.age2,3) p(sex*age1-4) ψ(age1-5) | 972.481 | 1.724 | 0.094 | 0.422 | 21 |
| $S^s$(age1-3)$S^W$(mass+sex*age2,3) p(sex*age1-4) ψ(age1-5) | 973.434 | 2.677 | 0.058 | 0.262 | 23 |
| $S^s$(age1-3)$S^W$(mass+sex*age2-4) p(sex*age1-4) ψ(age1-5) | 974.334 | 3.577 | 0.037 | 0.167 | 25 |
| $S^s$(age1-3)$S^W$(sex*age2,3) p(sex*age1-4) ψ(age1-5) | 974.516 | 3.758 | 0.034 | 0.153 | 22 |
| $S^s$(age1-3)$S^W$(sex*age2-4) p(sex*age1-4) ψ(age1-3) | 974.822 | 4.065 | 0.029 | 0.131 | 22 |
| $S^s$(age1-3)$S^W$(mass*sex*age2,3) p(sex*age1-4) ψ(age1-5) | 975.417 | 4.660 | 0.022 | 0.097 | 24 |
| $S^s$(age1-3)$S^W$(sex*age2-4) p(sex*age1-4) ψ(age1-5) | 975.439 | 4.682 | 0.021 | 0.096 | 24 |
| $S^s$(age1-3)$S^W$(mass+sex*age2-4) p(sex*age1-4) ψ(mass+age1-3) | 975.449 | 4.692 | 0.021 | 0.096 | 24 |
| $S^s$(mass+age1-3) $S^W$(mass+sex*age2,3) p(sex*age1-4) ψ(age1-5) | 975.625 | 4.868 | 0.020 | 0.088 | 25 |
| $S^s$(age1-3)$S^W$(mass*sex*age2-4) p(sex*age1-4) ψ(age1-5) | 976.167 | 5.410 | 0.015 | 0.067 | 26 |
| $S^s$(age1-3)$S^W$(sex*age2-4) p(sex*age1-4) ψ(sex*age1-3) | 976.373 | 5.616 | 0.013 | 0.060 | 25 |
| $S^s$(age1-3)$S^W$(mass*sex*age2-4) p(sex*age1-4) ψ(mass+age1-3) | 977.300 | 6.542 | 0.009 | 0.038 | 25 |
| $S^s$(mass+age1-3)$S^W$(mass*sex*age2-4) p(sex*age1-4) ψ(mass+age1-3) | 978.478 | 7.721 | 0.005 | 0.021 | 26 |
| $S^sS^W$(age1-3) p(age1-4) ψ(age1-5) | 979.084 | 8.327 | 0.004 | 0.016 | 14 |
| $S^s$(age1-3)$S^W$(sex*age2-4) p(age1-4) ψ(age1-3) | 980.026 | 9.269 | 0.002 | 0.010 | 18 |
| $S^sS^W$(age1-3) p(sex*age1-4) ψ(age1-5) | 980.435 | 9.678 | 0.002 | 0.008 | 18 |
| $S^s$(age1,2)$S^W$(mass+sex+age2,3) p(sex*age1-4) ψ(age1-3) | 981.059 | 10.302 | 0.001 | 0.006 | 18 |
| $S^sS^W$(mass+age1-3) p(age1-4) ψ(age1-5) | 981.224 | 10.467 | 0.001 | 0.005 | 15 |
| $S^s$(sex*age1-3)$S^W$(sex*age2-4) p(sex*age1-4) ψ(sex*age1-3) | 981.306 | 10.549 | 0.001 | 0.005 | 28 |
| $S^sS^W$(sex*age1-3) p(age1-4)ψ(sex*age1-5) | 987.427 | 16.670 | 0.000 | 0.000 | 22 |
| $S^sS^W$(age1-3) p(sex*age1-4) ψ(sex*age1-5) | 988.099 | 17.342 | 0.000 | 0.000 | 23 |
| $S^sS^W$(sex.age1-3) p(sex*age1-4) ψ(sex*age1-5) | 988.304 | 17.546 | 0.000 | 0.000 | 26 |
| $S^sS^W$(mass+sex*age1-3) p(age1-4) ψ(sex*age1-5) | 989.236 | 18.479 | 0.000 | 0.000 | 23 |
| $S^sS^W$(sex*age1-4) p(sex*age1-4) ψ(sex*age1-5) | 990.342 | 19.585 | 0.000 | 0.000 | 28 |
| $S^s$(sex*age1-4)$S^W$(sex*age2-4) p(sex*age1-4) ψ(sex*age1-5) | 992.424 | 21.667 | 0.000 | 0.000 | 34 |
| $S^s$(sex*age1-3)$S^W$(sex*age2,3) p(sex*coh+age1-3) ψ(sex*age1-3) | 1004.20 | 33.441 | 0.000 | 0.000 | 40 |
| $S^s$(sex*age1-4)$S^W$(coh.sex*age1-4) p(sex*age1-4) ψ(sex*age1-5) | 1009.26 | 38.503 | 0.000 | 0.000 | 50 |
| $S^s$(coh.sex*age1-3)$S^W$(coh.sex*age2,3) p(sex*age1-3) ψ(sex*age1-3) | 1047.41 | 76.653 | 0.000 | 0.000 | 66 |
| $S^s$(coh.sex*age1-3)$S^W$(coh+sex*age2,3) p(coh.sex*age1-3) ψ(coh.sex*age1-3) | 1065.93 | 95.174 | 0.000 | 0.000 | 81 |
| $S^s$(coh.sex*age1-4) $S^W$(coh.sex*age2-4) p(coh.sex*age1-4) ψ(coh.sex*1-4) | 1121.47 | 150.72 | 0.000 | 0.000 | 106 |
| Full model+basic constraints: age1($S^s = S^W$) $p^s = 1$ $\psi^{WS} = 0$ | 1242.37 | 271.61 | 0.000 | 0.000 | 139 |
| Full model | 1463.16 | 492.40 | 0.000 | 0.000 | 181 |

Table 2.2 – Model-averaged sighting probabilities and confidence intervals for weaned males and female aged 1 – 4.

| Sex and Age | Sighting Prob. | Lower Conf. Lim. | Upper Conf. Lim. |
|---|---|---|---|
| Males at age 1 | 0.317 | 0.199 | 0.466 |
| Males at age 2 | 0.608 | 0.420 | 0.768 |
| Males at age 3 | 0.781 | 0.573 | 0.905 |
| Males at age 4 | 0.999 | 0.966 | 1.000 |
| Females at age 1 | 0.549 | 0.374 | 0.712 |
| Females at age 2 | 0.667 | 0.499 | 0.801 |
| Females at age 3 | 0.821 | 0.641 | 0.922 |
| Females at age 4 | 0.747 | 0.583 | 0.862 |

# CHAPTER 3

# A LONGITUDINAL STUDY OF STELLER SEA LION NATALITY RATES IN THE GULF OF ALASKA WITH COMPARISONS TO CENSUS DATA[1]


## ABSTRACT

Steller sea lion (*Eumetopias jubatus*) numbers in the western distinct population segment are beginning to recover following the dramatic decline that began in the 1970s and ended around the turn of the century. Low female reproductive rates (natality) may have contributed to the decline and remain an issue of concern for this population. During the 2000s we found high natality among Steller sea lions in the Gulf of Alaska indicating a healthy population. This study extends these previous estimates over an additional three years and tests for interannual variations and long-term trends. We further examine the proportions of pups to adult females observed on the rookery and nearby haulouts during the birthing season to assess whether census data can be used to estimate natality. Open robust design multistate models were built and tested using Program MARK to estimate survival, resighting, and state transition probabilities in addition to other parameters dependent on whether or not a female gave birth in the previous year. Natality was estimated at 70% with some evidence of interannual variation but a long-term increasing or decreasing trend was not supported by the data. Bootstrap and regression comparisons of census data with natality estimates revealed no correlation between the two methods suggesting that census data are not an appropriate proxy for natality in this species. Longitudinal studies of individual animals are an appropriate method for estimating vital rates in


[1] Maniscalco JM, Springer AM, Parker P, Adkison MD (2014) A longitudinal study of Steller sea lion natality rates in the Gulf of Alaska with comparisons to census data. PLoS ONE 9(11):e111523, November 10, 2014.

species with variable detection over time such as the Steller sea lion. This work indicates that natality remains high in this region and is consistent with a population in recovery.

## INTRODUCTION

Over the past 2 centuries, several fur seal and sea lion (Otariidae) populations have recovered to healthy numbers following catastrophic collapses [1]. Steller sea lions (*Eumetopias jubatus*) in Alaska, USA may be emulating this trend as numbers over a large portion of the western distinct population segment (WDPS) have begun to increase in recent years following a precipitous 30-year decline that started in the early 1970s [2,3]. Indeed, Steller sea lion populations may have undergone dramatic fluctuations in abundance several times during the past 4 millennia [4]. The most recent decline is primarily attributed to reduced juvenile survival during the 1980s in addition to minor reductions in reproductive rates and adult survival [5-7]. Changes in those vital rates could have resulted from nutritional stress, killer whale (*Orcinus orca*) predation, or a combination of these and other factors such as direct interactions with fisheries [8-11]. The latest upswing in Steller sea lion numbers was estimated to have begun in the early 2000s [12] and may be attributed to improved juvenile survival [13] and high natality rates that are reflective of a healthy population [14]. However, some work based on population demography and theoretic modeling has suggested natality reached an all-time low during the past decade [15].

Continued monitoring of vital rates is essential for species of concern such as the WDPS of Steller sea lions, which is classified as endangered under the Endangered Species Act. Of the two approaches to obtaining vital rate information, longitudinal, individual-based studies have many advantages over cross-sectional, population-level studies [16]. Yet, published estimates of

vital rates based on longitudinal studies are rare for the WDPS of Steller sea lions even though hundreds of millions of dollars have been dedicated to researching these animals. Here we provide an update of our previous work [14] on natality rates for these animals in the Gulf of Alaska based on a longitudinal study of adult females and assess the potential for using census data (counts) to predict trends in natality over time.

Natality is defined as the birthrate or the proportion of births to some segment of the general population – generally mature females. Female Steller sea lions become reproductively mature at three to seven years of age and give birth to one pup per year but not necessarily every year [17]. The birthing season typically ranges between late May and early July in Alaska [18]. Twinning is extremely rare [19] and juveniles are often weaned during the spring months at age 1, age 2 or even older [13,20]. However, natality does not include neonatal or juvenile survival, and it is important to differentiate these life history variables because of the widely different factors that may affect them. Low rates of natality among pinnipeds have been related to disease, contaminants, and poor nutrition [6,21], whereas neonatal or juvenile survival may be more influenced by weather conditions, predation, or food limitation [22-24]. By lumping life history stages together, information pertinent to understanding population dynamics can be hidden or lost entirely.

We previously outlined several reasons why it may be difficult to estimate natality based on proportions of pups on rookeries and haulouts late in the breeding season [14]. Primarily, these are uncertainties about the extent of neonatal mortality due to storm waves for example, and proportions of females foraging at sea which may change systematically with shifting oceanic regimes [14]. Assuming stability in these variables over time might lead to erroneous conclusions about the proportion of pups that are born to a population of sea lions. We further

suggested that disparities in natality estimation techniques may be resolved by long-term comparisons of census data with direct estimates of natality based on longitudinal observations of adult females and mark-recapture modeling [14]. In this study, we added 3 additional years to our previous time series and extended our natality estimates over a 10-yr period, 2003 – 2012, using robust-design mark-recapture statistics. We further compared these results to census counts of the proportion of pups to adult females on rookeries and haulouts to determine if census data can be used to predict trends in natality. If proportions of pups to adult females, or non-pups, can be used to predict natality, we should expect positive correlations between these proportions and mark-recapture estimates of natality over time.

## MATERIALS AND METHODS

### *Ethics Statement*

This research was conducted in accordance with Alaska SeaLife Center Institutional Animal Care and Use Committee Protocol No. R10-03-01 and National Marine Fisheries Service Permit No. 14324 for research on endangered Steller sea lions. The Chiswell Island group is part of the U.S. Fish and Wildlife Service National Maritime National Wildlife Refuge. Research was conducted on refuge lands under Right-of-Way Permit No. M-344-AM and Special Use Permit No. 74500-10-001 and earlier versions.

### *Study Site and Observational Methods*

The focal area of this research included the Steller sea lion rookery on Chiswell Island (59° 59.18' N, 149° 23.40' W) and nearby haulouts in Kenai Fjords (Figure 3.1), which lie within the range of the endangered WDPS. The population decline at the Chiswell rookery was similar

to that of other rookeries in the central Gulf of Alaska – that is, abundance fell by 90% from 1,106 adults in 1976 [25] to approximately 90 adults and 50-80 pups in the 2000s [26]. Beginning in 1999, up to six remotely operated video cameras were used to monitor Steller sea lions (see [26] for details). Video images, which provided complete spatial coverage of the Chiswell Island rookery, were viewable and controllable in real-time from the Alaska SeaLife Center 65 km away. Cameras were also installed and monitored at nearby haulouts beginning in 2000 (Figure 3.1).

Most adult Steller sea lions can be individually identified by unique scars, fungal patches, and/or flipper patterns, and longitudinal studies have been successfully conducted on animals identified by such means [23,24,26,27]. Over the course of this study, female sea lions with unique markings (n = 184) were tracked and digital photos of these animals and their distinguishing marks were taken on a regular basis (at least twice per month) at all remotely-monitored sites in Kenai Fjords. Some breeding females were identified by flipper tags (n = 5) or brands (n = 16), and age was known only for these animals. Females that did not have at least two distinguishing marks and could not be reliably resighted from one year to the next were not used in the analysis. Although pictures and data for some females were collected as early as 1999, the period 1999-2002 was not considered in the analysis of natality rates because there was a more focused effort on sighting females giving birth over females that did not. All females with unique markings were tracked from 2003 onward whether or not they gave birth.

Our observations were conducted year-round but intensified during the birthing and breeding season beginning in mid-May. Hour-long scan sampling for identifiable females and their pups was conducted four to ten times daily from 0600 h to 2200 h; earlier and later hours were added around the summer solstice (21 June) when light levels were sufficient for viewing

sea lions. After 10 August, observations were recorded from approximately sunrise to sunset as diminishing daylight allowed. Events such as births and deaths were opportunistically recorded as they occurred or within 4 hrs of their known occurrence [24,26]. Births that happened overnight were recorded the following morning as having occurred at the half-way point of non-observation hours.

Complete census counts of all sea lions by age class (adult males, adult females, juveniles 1 – 4 yrs old, and pups 0 – 1 yrs old) on the rookery and at two nearby haulouts (Figure 3.1) were made at approximately 1100 h throughout the breeding season. Ratios of pups to adult females on the rookery and haulouts were summarized between 25 June and 15 July each year to determine if these counts could be used as a proxy for natality rates. This date range corresponds to when the National Marine Fisheries Service conducts their range-wide flight surveys for population counts [2,28] which are used in some models for vital rates estimation [7,15]. In some cases when census counts were not conducted ($\leq 2$ each yr; 14 out of 208 total), daily numbers of each age class were interpolated from previous and subsequent counts.

Steller sea lion mothers in the WDPS will normally remain with their newborn pups for 8 to 12 days following parturition [26,27]. Given the duration and detail of observations in this study (frequent scans and complete spatial coverage of the rookery), it is highly unlikely that any births went unnoticed. Furthermore, females that give birth to stillborns are not normally considered to be productive nor are stillbirths considered in the definition of natality. However, we include full-term stillbirths in our analysis (approximately 2%; [24]) so that our estimates are comparable to historic estimates during the 1970s when the population was presumed healthy and in the 1980s during the height of the decline in this region. Those earlier estimates were based on late-term pregnancies of adult females collected in the field and could not account for

stillbirths [6]. In addition, those previous studies only considered reproductively mature females whose status was known by examination of copora lutea in ovaries [6,17]. It was neither possible nor the intention of this study to verify reproductive maturity for females that were not observed to give birth even when age was known. Therefore, females of known age were included in this study beginning at 5 years of age to be consistent with the average age of sexual maturity of 4.6 yrs [17], which would indicate that age of first pupping would be at about 5.6 yrs. Females of unknown age were included in this study if they were judged to be at least 4 yrs of age as approximated by visual size comparisons to other known-age females lying nearby.

Non-breeding haulouts within the study area were also monitored during the birthing season to account for females that may have spent more time at those locations and to reduce sample bias toward more fecund females that may spend more time at the rookery seasonally and across years. Females at haulouts were included in the analyses if they met the aforementioned sighting and maturity criteria. Adult females that were observed without a pup during any birthing season were classified as not giving birth whether on the rookery or a haulout. However, some of the animals in the Chiswell Island population that were not giving birth on the rookery in any given year spent the summer elsewhere, presumably outside of the study area. Adult females that returned to the study area later in the year were typically without a pup but a few (< 2%) did return with a suckling pup indicating that they gave birth elsewhere. Therefore, females that were without a pup when observed only during the non-pupping season could not be defined with certainty as not giving birth during the previous summer. We were able to account for this uncertainty by modeling the data as a hidden Markov process using a multi-state robust design [29].

*Data Analysis*

Open robust design (ORD) multi-state models with state uncertainty and seasonal effects were constructed and run using Program MARK [30]. Data were modeled across 10 primary periods (years 2003 – 2012) and 4 secondary periods – summer (Jun-Aug), autumn (Sep-Nov), winter (Dec-Feb), and spring (Mar-May) for a total of 40 sampling occasions. For each occasion, the states of every female were recorded as "b" – observed birth or with pup, "n" – observed but did not give birth, "0" – not observed, and "u" – observed during the non-birthing season without a pup, state uncertain. ORD models allow for entry and departure from the study area between primary periods and secondary periods, as often occurs among sea lions between seasons, but these models also greatly increase the number of parameters that can be estimated compared to models without a robust design. Nevertheless, robust design models allow estimation of temporary emigration from the study area and provide more precise estimates of survival and state transitions [29,31,32]. Furthermore, multistate ORD models do not necessarily require that the state of females be known with certainty or that females with and without a pup have equal sighting probabilities [31,33]. A goodness of fit test for multi-state ORD models when both states are observable has not been developed. However, a goodness of fit test using a simpler modeling approach for much of these data has shown only a slight and insignificant degree of overdispersion [14], and we have no reason to believe that data in the current model structure are much different.

The following parameters were estimated for this study with some initial constraints that were appropriate for the behavioral biology of Steller sea lions and to keep model run times reasonable:

$S_i^x$ = probability that a female in state x in year *i* survives until *i* + 1.

$p_i^x$ = probability that a female is sighted in time period *i* in state x, given that she is present in the study area in period *i*. For secondary sampling periods a scaled covariate was added to reflect seasonal changes in observer effort which was highest during summer and lowest during winter.

$\psi_i^{xy}$ = transition probability or probability that a female in state x in year *i* is in state y in year *i* + 1, given that she survived from year *i* to *i* + 1.

$\pi_t^x$ = probability that a female is first observed in state x in year *i* for years 2 – 9 of the study.

$\omega_t^x$ = probability that a female is in state x in year *i*, used as an estimate of natality in this study.

$\delta_t^x$ = probability that a female is classified correctly to state. Constrained to be equal across all times periods for females with a pup. Constrained to be equal for females not seen with a pup across primary periods but allowed to vary between 1$^{st}$ secondary period (summer) and 2$^{nd}$ – 4$^{th}$ secondary period combined.

$pent_t^x$ = probability that a female in state x enters into the study area between a given secondary period. Constrained to be equal across primary periods for both states but allowed to vary between states and secondary periods with the mlogit link function to sum to $\leq 1$.

$d_t^x$ = probability that a female in state x departs from the study area between secondary periods. Constrained to be equal across primary periods but allowed to vary between states and between secondary periods.

$\alpha_t^x$ = probability that the attribute for state assignment has appeared (i.e., pup). Constrained to 1 for the 1$^{st}$ secondary period and to 0 for all other sampling periods because females only give birth during summer.

$c_t^x$ = probability that the attribute ceases – i.e., pups are weaned. Weaning often occurs during the spring months [20] and therefore was fixed to 0 for the 1st and 2nd secondary period intervals and allowed to vary during the 3rd interval.

These model parameters were combined across primary and secondary sampling periods into a joint multinomial likelihood using the mlogit link function in Program MARK. Additional constraints were placed on the models with regard to biological relevance in the search for parsimony. For example, survival (S) and state transitions ($\psi^{xy}$) were constrained to be equal over time in some models to assess whether the data more closely fit those model structures compared to time-varying model structures. The average ratio of pups to adult females on Chiswell Island and nearby haulouts was included as an annual covariate in some models to assess the effect on model fit. In the same manner, the total numbers of pups born on Chiswell each year was included as annual covariate for female state ($\omega$) in addition to modeling linear trends. All models were compared with Akaike's Information Criteria (AIC; [34]), corrected for small sample bias (AICc; [35]). AICc weights, calculated from model differences in AICc values ($\Delta$AICc), indicated relative support for the various models. Likelihood ratio tests (LRT) were also run to test for meaningful differences in models of interest. Finally, all models were averaged (multimodal inference; [36]) for estimates of parameter values relevant to this study.

We further assessed the possibility of using ratios of pups to females observed on rookeries and haulouts as a proxy for natality rates. Census data were log transformed to approximate normality and the ratios, *ln* (pups) / *ln* (adult females), were regressed against natality rates estimated from the ORD analysis for each year. This was conducted for each of 21 days between 25 June and 15 July each year to determine if any of these days provide a more

accurate representation of natality over other days in that time period. We also conducted a bootstrap randomization test on standardized census data. The pup / adult female ratio was standardized to remove intra-seasonal patterns of haulout use by subtracting the daily means across years and adding back the overall mean to the daily count. We ran 1000 iterations to compare with estimated natality rate for the corresponding year. If count ratios are representative of natality rates across years, we would expect to find a significant correlation between these variables.

**RESULTS**

A total of 16 models were run and ranked in order of lowest AICc score (Table 3.1). Models with no time differentiation in survival (S), sighting probability (p), and state transitions ($\psi$) showed more support for the data compared to those with variation across years (primary sampling periods). Time variation across seasons (secondary periods) was retained for sighting and departure (d) probabilities due to seasonal movements into and out of the study area (Alaska SeaLife Center, unpublished data), and the desire to model these changes. There was some evidence of differences in survival between females giving birth (89.0 ± 1.4%) and those that did not (86.1 ± 2.4%) as variation in this state was expressed in two of the four best models with no significant differences (Table 3.2; LRT: Model 1 vs 2: $\chi^2 = 1.602$; $P = 0.206$; Model 3 vs 4: $\chi^2 = 1.107$; $P = 0.293$). There was also little evidence of annual variation in the proportion of females giving birth ($\omega^b$) as noted in a comparison of Models 1 and 3 (Table 3.1; LRT: $\chi^2 = 16.940$; $P = 0.050$) and Models 2 and 4 (Table 3.1; LRT: $\chi^2 = 16.444$; $P = 0.058$). See also Table 3.2 for time varying differences in $\omega^b$ for models 3 and 4.

An *a priori* decision was made to test for an increasing trend in natality, as the population in this region had been increasing over the study period [2]. However, fitting a linear increasing trend to natality did not improve model fit (Model 10 vs Model 4). Upon examination of natality estimates from the top ranked models, it was determined that a linear decrease in natality should also be tested for, but this also did not improve model fit (Model 11). We further tested for an improvement in model fit using either the total number of pups born or the average ratio of pups to adult females as linear covariates for $\omega^b$ each year. Both greatly reduced model fit compared to the model with full time dependence in $\omega^b$ (Models 5 & 6 vs Model 3 and Models 8 & 12 vs Model 4).

The four best models held 99.9% of the total weight (Table 3.1) and therefore, model averaged parameter estimates were based primarily on these structures. Survival to a subsequent year for females giving birth ($S^b$; 88.49 ± 1.33% SE) was slightly higher than for those that did not give birth ($S^n$; 87.27 ± 2.06%). Sighting probabilities were higher for females giving birth ($p^b$) compared to those without a pup ($p^n$) and seasonal sighting probabilities were especially low during winter (Table 3.2). Natality rates ($\omega^b$) were high with an overall average of 70.5 ± 1.6% that ranged narrowly from 67.6% ± 5.7% to 74.5% ± 7.3% (Figure 3.2). Also, females that gave birth in year *i* were nearly as likely to give birth in year *i* +1 ($\psi^{bb} = 0.708 \pm 0.021$) as females that did not give birth in year *i* ($\psi^{nb} = 0.736 \pm 0.033$).

Natality based on the ratio of pups to adult females on the rookery and nearby haulouts was higher than estimates from the mark-recapture modeling and had greater variation (91.3% ± 3.2%; Figure 3.2). Estimates for some years were unrealistically >100% because varying numbers of adult females were foraging at sea and unavailable to be counted. However, the intent of this analysis was not to obtain exact estimates of natality but to determine if natality

rates based on census counts are correlated with direct estimates of natality and could therefore be used as a meaningful proxy for changes in natality. To test for a correlation, those rates were regressed against the natality rates ($\omega^b$) estimated from Program MARK for each year. Slopes of the 21 regressions ranged from -0.250 to +0.223 and none were significant ($P$-value range: 0.080 – 0.925). The bootstrap analysis of the pup/adult female ratios also resulted in a non-significant relationship with natality ($r^2 = 0.048$; $P = 0.542$) and had slopes centered on zero (Figure 3.3).

## DISCUSSION

### *Mark-Recapture Parameter Estimates*

We previously examined natality of Steller sea lions in this region over seven years using a standard mark recapture multistate approach without robust design [14]. The current analysis was undertaken to improve our estimates using the robust design, to examine possible interannual and long-term changes in natality, and to assess the use of census data as a proxy for natality.

Not surprisingly, estimates of natality were similar to those previously found in this region at about 70% but with a smaller standard error (1.6 vs. 2.5%; [14]), which may be due partly to the larger sample size in this study. In addition, parameter estimates such as these are notably improved using the robust design as reported by others [29,32]. Sighting probabilities were high during the summer months for females giving birth and for those not giving birth in any given year (Table 3.2). Yet many non-breeders were not observed on the rookery during the birthing season (mid-May to Mid-July) and arrived later in the summer or autumn. If we only considered sightings during the birthing season much of the information about non-breeders would be lost and hence lead to greater uncertainty in our estimates.

Natality was not much different from pre-decline levels (67%) but better than estimated during the height of the population decline (55%) in the Gulf of Alaska during the 1980s [6]. It has previously been suggested that natality rates bottomed out at about 43% in the early 2000s, as estimated from an inferential population dynamic model [15]. A rapid change in natality from percentages in the mid-40s to nearly 70% would seem quite unusual; hence, it was of interest to test for an increasing trend in this study. However, the model we tested with an increasing trend in natality did not fit the data, nor did one with a decreasing trend. In our analysis, natality ranged narrowly around 70%, with 2 of the 4 best models supporting interannual fluctuations but no trends. Therefore, we have little evidence to support unusually low natality rates during any year of this study.

Notwithstanding variation in survival, natality rates of 60% to 75% have been generally associated with stable or increasing populations of pinnipeds [37-40], including the eastern distinct population segment (EDPS) of Steller sea lions [41]. Natality of 55% or lower has been associated with declining populations of otariids and related to the adverse effects of density dependant factors such as intraspecific competition for food or breeding space [6,42], but see also [43]. Therefore, our estimate of natality from the Chiswell Island population of Steller sea lions is indicative of a population where adult females seemingly are not under resource limitation. Populations in this region and as far west as the eastern Aleutian Islands have been increasing since the early 2000s [2]. We cannot say with certainty that natality rates estimated here in the eastern Gulf of Alaska are representative of natality as far west as the eastern Aleutian Islands, but given the similar population trends [2], we currently have no reason to suppose otherwise.

During periods of food limitation long-lived mammals may exhibit a cost of reproduction in terms of reduced probability of survival or reproduction in successive years compared with times of food abundance [44,45]. Such a cost likely affected Steller sea lions during the 1980s when pregnancy was negatively correlated with lactation status [6]. Similar to our previous work [14], we found no evidence of a cost of reproduction among Steller sea lions during the period of this study (2003 – 2012) with survival and subsequent reproduction not being correlated with previous birthing status. This finding is consistent with a healthy population that is not exhibiting signs of broad scale food limitation [8,45,46].

*Comparisons with Census Data*

Long-term census-based studies provide important information regarding changes in demographics, distribution, densities, and trends of wildlife populations including the potential influences of climate change and human activities [16]. However, using census data to estimate vital rates in variably detectable species such as pinnipeds that spend a large proportion of their time foraging at sea may be difficult. Using several methods, we were unable to find a correlation between either pup counts or pup to female ratios and our natality estimates. As our natality estimates showed little year to year variation, this could have made such relationships difficult to detect. Nevertheless, if census counts can be used as a proxy for natality, we could expect at least weak positive correlations, but they were strongly centered on zero (Figure 3.3).

Using census counts for modeling vital rates is unusual for many large vertebrates and caution is warranted when modeling such data for vital rate estimates [47]. Census counts of Steller sea lions can vary with tide height, storm waves, time of day, and food availability [48-50]. Pup counts may or may not reflect the actual number of births because storm waves during

the peak of birthing are variable across years and can cause huge losses of neonates [23,24]. Those variations are typically assumed to be consistent over time [7,15] but they are not [14]. This is a primary reason why census data cannot be reliably used to estimate vital rates in species such as Steller sea lions unless adjustments are made to the data that appropriately reflect environmental stochasticity over time.

Accounting for variation in sighting probabilities is integral to longitudinal studies employing mark-recapture analysis. Long-term studies of a representative sample of individuals are necessary for accurate estimates of age-specific survival and natality, but are invariably more time consuming and costly than snapshot population counts [16,51]. Nevertheless, these mark-recapture methods provide critical information for understanding life histories and behavior of species of concern. In addition to natality, survival, and sighting probabilities, many other parameters can be estimated with the mark-recapture data analysis techniques currently available [29,32,33]. For instance, longitudinal studies of branded Steller sea lions are providing insights into temporary and permanent migration between the distinct population segments [52]. Without such work, we might mistakenly assume that populations receiving such immigrants were increasing solely due to improved survival or natality.

Census counts provide information on population trends over time, whereas individual-based longitudinal studies will more specifically inform researchers of why and how populations are changing. Based on census count data, we know that the EDPS of Steller sea lions has been increasing over the past 30 years [53]. Based on longitudinal studies we also recognize that the population increases likely result from a combination of good juvenile survival [54], good natality [41], and some immigration from the WDPS [51]. All of this information and more has led to the recent delisting of the EDPS from the Endangered Species List [55]. The WDPS

remains endangered, but with population trends continuing to increase, downlisting to threatened status is possible by 2015 [2]. Current population growth in the WDPS can be attributed to good natality and adult survival ([14]; this study) in addition to improved juvenile survival [13] since the height of the decline. Continued monitoring of vital rates is essential to detect changes that could threaten recovery of the species. Longitudinal studies of this nature can detect changes in vital rates that may happen quickly and drastically in response to increasing environmental stochasticity in the face of a shifting global climate [56].

## ACKNOWLEDGMENTS

Data collection for this study was accomplished by many hard-working technicians and interns at the ASLC including Melinda Fowler, Karin Harris, Juliana Kim, Carlene Miller, Emily Teate, and many other technicians and interns. We thank them and Lara Horstmann and Chuck Frost for discussions, commentaries, and much helpful advice on this material. Chris Oosthuizen also provided very constructive comments on the manuscript.

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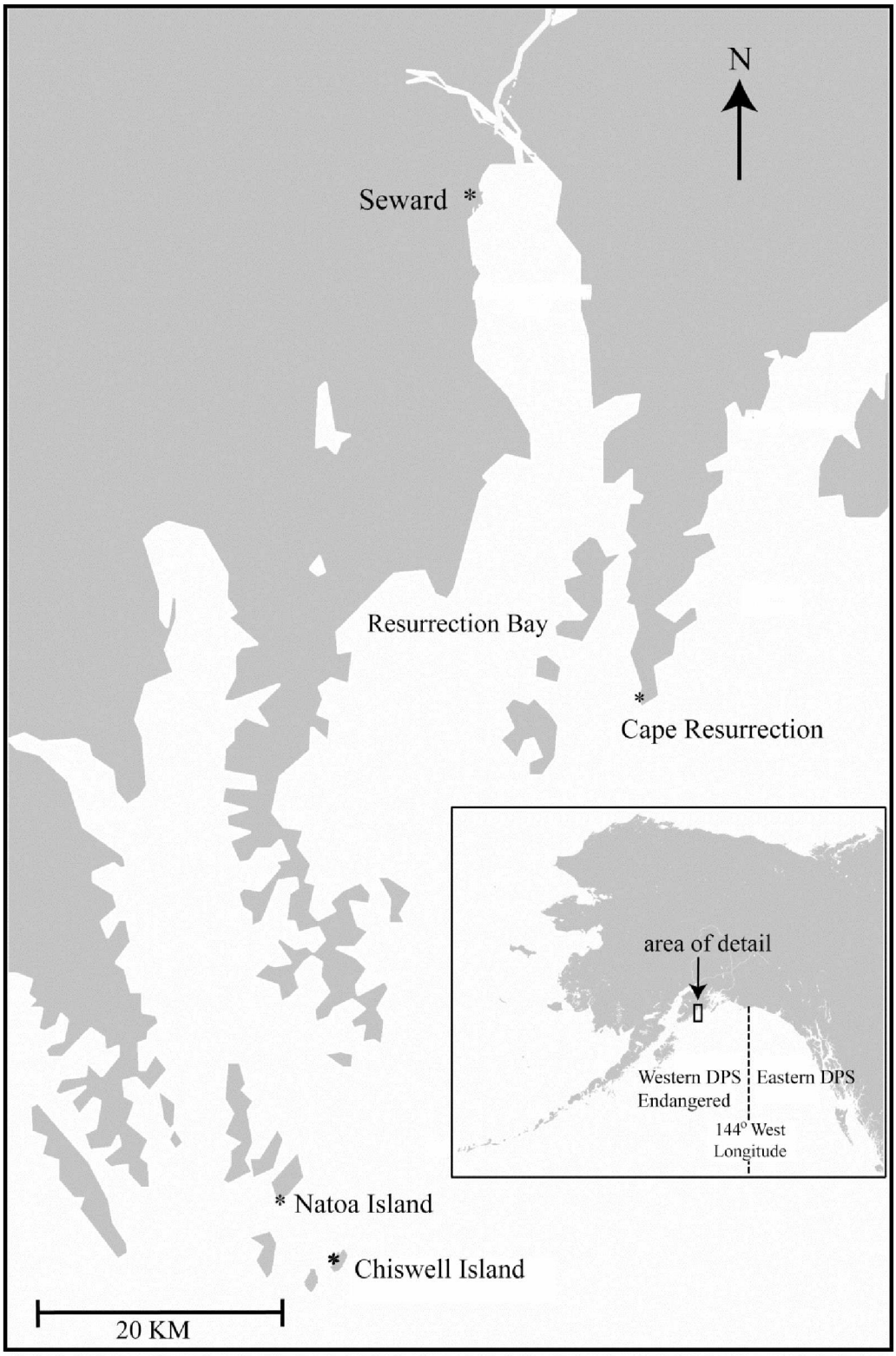


Figure 3.1 – Location of the Chiswell Island Steller sea lion rookery and remotely monitored haulouts at Cape Resurrection and Natoa Island in Kenai Fjords, Gulf of Alaska.

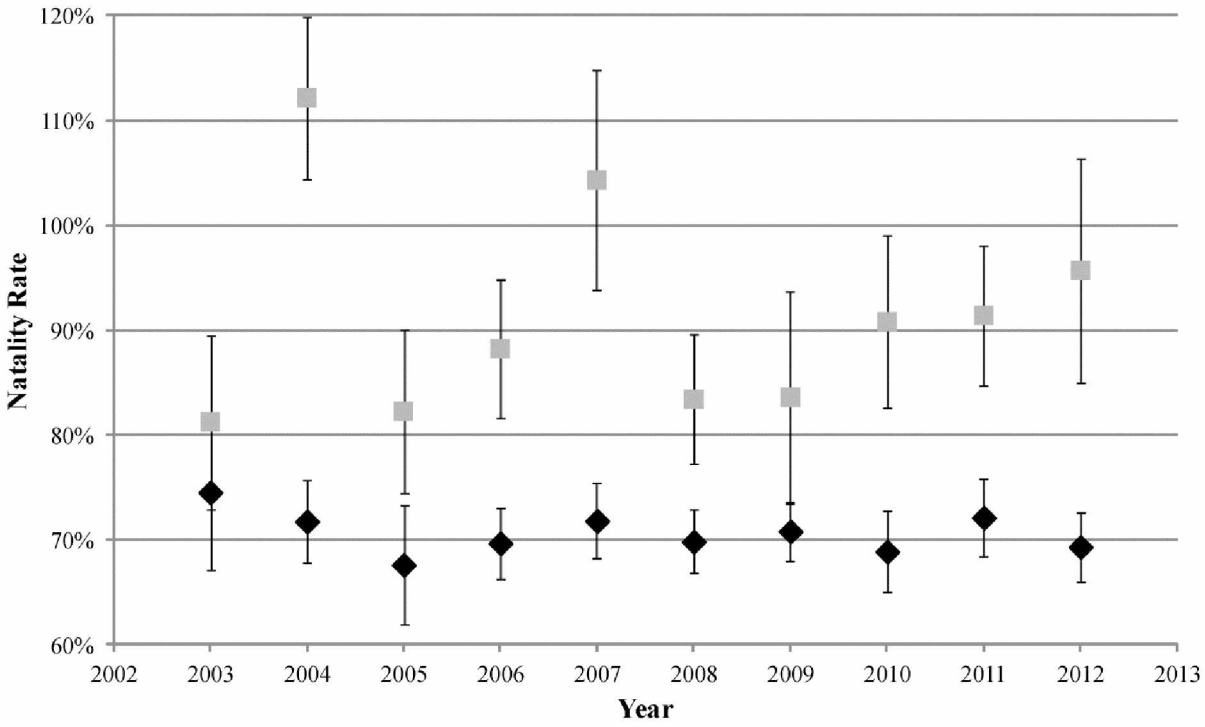


Figure 3.2 – Mark-recapture estimates of natality rates (black diamonds) and natality estimates based on census data (gray squares) for adult female Steller sea lions at the Chiswell Island rookery from 2003 to 2012 with 95% confidence intervals. Note that the mark-recapture estimates are different from estimates expressed in Table 2 due to model averaging.

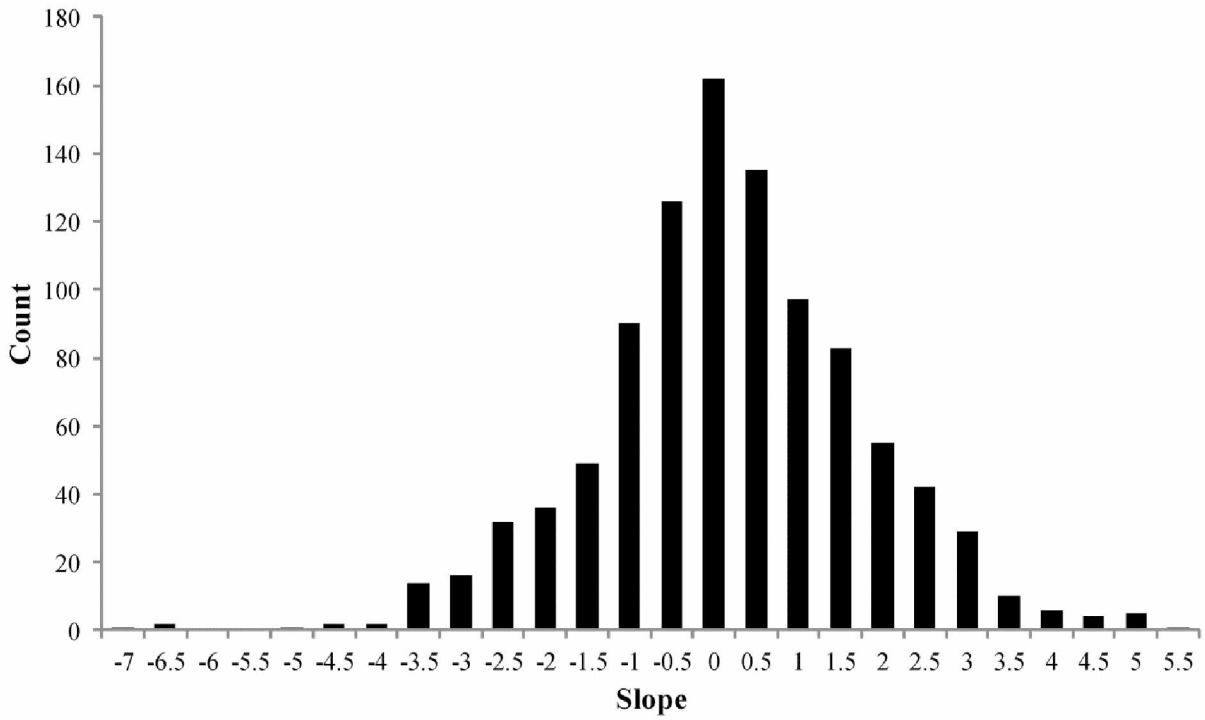


Figure 3.3 – Bootstrap histogram of regression slopes based on pup to adult female ratios versus mark-recapture natality estimates. This figure shows that the regression slopes were strongly centered on zero with no correlative trend.

Table 3.1 – Comparison of models tested using a multi-state open robust design in Program Mark for estimation of survival (S), sighting probabilities (p), state transitions ($\psi$), and state occupation ($\omega$) among Steller sea lions in Kenai Fjords. Proportion of the population released in each state ($\pi$) and departure probabilities (d) were also manipulated to test their effects on model fit. Initial constraints on parameters not listed here are outlined in the Methods.

| Model Rank | Model Structure | No. Param. | AICc | ΔAICc | AICc Weights | Model Likelihood |
|---|---|---|---|---|---|---|
| **1** | $S_{.}\ p_{st.2^\circ}\ \psi_{st.}\ \pi_{.}\ \omega_{.}\ d_{st.2^\circ}$ | 30 | 6106.846 | 0.000 | 0.4067 | 1.0000 |
| **2** | $S_{st.}\ p_{st.2^\circ}\ \psi_{st.}\ \pi_{.}\ \omega_{.}\ d_{st.2^\circ}$ | 31 | 6107.313 | 0.467 | 0.3220 | 0.7916 |
| **3** | $S_{.}\ p_{st.2^\circ}\ \psi_{st.}\ \pi_{.}\ \omega_{t}\ d_{st.2^\circ}$ | 39 | 6108.617 | 1.771 | 0.1678 | 0.4125 |
| **4** | $S_{st.}\ p_{st.2^\circ}\ \psi_{st.}\ \pi_{.}\ \omega_{t}\ d_{st.2^\circ}$ | 40 | 6109.601 | 2.755 | 0.1026 | 0.2522 |
| **5** | $S_{.}\ p_{st.2^\circ}\ \psi_{st.}\ \pi_{.}\ \omega_{p}\ d_{st.2^\circ}$ | 39 | 6119.334 | 12.488 | 0.0008 | 0.0019 |
| **6** | $S_{st.}\ p_{st.2^\circ}\ \psi_{st.}\ \pi_{.}\ \omega_{r}\ d_{.2^\circ}$ | 39 | 6124.224 | 17.378 | 0.0001 | 0.0002 |
| **7** | $S_{st.}\ p_{st.2^\circ}\ \psi_{st.}\ \pi_{t}\ \omega_{t}\ d_{st.2^\circ}$ | 47 | 6124.259 | 17.413 | 0.0001 | 0.0002 |
| **8** | $S_{st.}\ p_{st.2^\circ}\ \psi_{st.}\ \pi_{.}\ \omega_{r}\ d_{st.2^\circ}$ | 40 | 6125.533 | 18.687 | 0.0000 | 0.0001 |
| **9** | $S_{.t}\ p_{st.2^\circ}\ \psi_{st.}\ \pi_{t}\ \omega_{t}\ d_{st.2^\circ}$ | 54 | 6129.711 | 22.865 | 0.0000 | 0.0000 |
| **10** | $S_{st.}\ p_{st.2^\circ}\ \psi_{st.}\ \pi_{.}\ \omega_{up}\ d_{st.2^\circ}$ | 40 | 6133.919 | 27.073 | 0.0000 | 0.0000 |
| **11** | $S_{st.}\ p_{st.2^\circ}\ \psi_{st.}\ \pi_{.}\ \omega_{dn}\ d_{st.2^\circ}$ | 40 | 6136.540 | 29.694 | 0.0000 | 0.0000 |
| **12** | $S_{st.}\ p_{st.2^\circ}\ \psi_{st.}\ \pi_{.}\ \omega_{p}\ d_{st.2^\circ}$ | 40 | 6136.540 | 29.694 | 0.0000 | 0.0000 |
| **13** | $S_{st.}\ p_{st.2^\circ}\ \psi_{st.}\ \pi_{.}\ \omega_{t}\ d_{.2^\circ}$ | 37 | 6138.479 | 31.634 | 0.0000 | 0.0000 |
| **14** | $S_{st.t}\ p_{st.2^\circ}\ \psi_{st.}\ \pi_{t}\ \omega_{t}\ d_{st.2^\circ}$ | 63 | 6139.086 | 32.241 | 0.0000 | 0.0000 |
| **15** | $S_{st.t}\ p_{st.2^\circ}\ \psi_{st.t}\ \pi_{t}\ \omega_{t}\ d_{st.2^\circ}$ | 79 | 6156.477 | 49.632 | 0.0000 | 0.0000 |
| **16** | $S_{st.t}\ p_{st.1^\circ.2^\circ}\ \psi_{st.t}\ \pi_{t}\ \omega_{t}\ d_{st.2^\circ}$ | 151 | 6190.485 | 83.639 | 0.0000 | 0.0000 |

*Notes*: Subscripts indicate state variation (st; with vs without pup), time variation (t), and increasing (up) or decreasing (dn) linear trends across primary periods in addition to time variation specific to primary periods (1°) and secondary periods (2°). Additional subscripts identify annual covariates of total number of pups born (p) and the average ratio of pups to adult females (r) observed.

Table 3.2 – Estimates (± 1 SE) from the four top-ranked models in Table 1 for survival of females that gave birth ($S^b$) and those that did not ($S^n$), occupation of birthing state ($\omega^b$) in any given year, and sighting probabilities by season for females that gave birth ($p^b$) and those that did not ($p^n$).

| Parameter | Model 1 | Model 2 | Model 3 | Model 4 |
|---|---|---|---|---|
| $S^b$ | 88.1% (1.2%) | 89.0% (1.4%) | 88.1% (1.2%) | 89.0% (1.4%) |
| $S^n$ | 88.1% (1.2%) | 86.1% (2.4%) | 88.1% (1.2%) | 86.1% (2.4%) |
| $\omega^b$ – 2003 | 70.5% (1.6%) | 70.5% (1.6%) | 85.5% (5.0%) | 85.5% (5.0%) |
| $\omega^b$ – 2004 | 70.5% (1.6%) | 70.5% (1.6%) | 75.3% (5.7%) | 75.3% (5.7%) |
| $\omega^b$ - 2005 | 70.5% (1.6%) | 70.5% (1.6%) | 60.0% (5.7%) | 60.0% (5.7%) |
| $\omega^b$ – 2006 | 70.5% (1.6%) | 70.5% (1.6%) | 67.6% (5.4%) | 67.6% (5.4%) |
| $\omega^b$ – 2007 | 70.5% (1.6%) | 70.5% (1.6%) | 75.5% (4.7%) | 75.5% (4.7%) |
| $\omega^b$ – 2008 | 70.5% (1.6%) | 70.5% (1.6%) | 68.2% (4.8%) | 68.2% (4.8%) |
| $\omega^b$ – 2009 | 70.5% (1.6%) | 70.5% (1.6%) | 71.8% (4.6%) | 71.8% (4.6%) |
| $\omega^b$ – 2010 | 70.5% (1.6%) | 70.5% (1.6%) | 64.7% (4.9%) | 64.7% (4.9%) |
| $\omega^b$ – 2011 | 70.5% (1.6%) | 70.5% (1.6%) | 76.6% (4.2%) | 76.6% (4.2%) |
| $\omega^b$ – 2012 | 70.5% (1.6%) | 70.5% (1.6%) | 66.3% (4.6%) | 66.3% (4.6%) |
| $p^b$ – summer | 99.9% (<0.1%) | 99.9% (<0.1%) | 99.9% (<0.1%) | 99.9% (<0.1%) |
| $p^n$ – summer | 98.3% (0.9%) | 97.7% (1.2%) | 97.7% (1.2%) | 97.7% (1.3%) |
| $p^b$ – fall | 94.6% (1.8%) | 94.6% (1.8%) | 94.6% (1.8%) | 94.6% (1.8%) |
| $p^n$ – fall | 74.3% (4.9%) | 72.8% (4.4%) | 72.9% (4.4%) | 72.8% (4.4%) |
| $p^b$ – winter | 24.6% (3.6%) | 24.6% (3.6%) | 24.6% (3.6%) | 24.6% (3.6%) |
| $p^n$ – winter | 12.7% (2.3%) | 14.3% (4.0%) | 14.3% (4.0%) | 14.3% (4.0%) |
| $p^b$ – spring | 70.4% (4.1%) | 70.4% (4.1%) | 70.4% (4.1%) | 70.4% (4.1%) |
| $p^n$ – spring | 39.4% (4.2%) | 40.1% (4.7%) | 40.1% (4.7%) | 40.1% (4.7%) |

# CHAPTER 4

# PROJECTING THE POPULATION TREND OF STELLER SEA LIONS IN THE EASTERN GULF OF ALASKA WITH ESTABLISHED VITAL RATES AND LIFE TABLES


## ABSTRACT

Steller sea lion (*Eumetopias jubatus*) numbers are beginning to recover across most of the western distinct population segment following catastrophic declines that began in the 1970s and ended around the turn of the century. This study makes use of currently established vital rates from a trend-site rookery in the eastern Gulf of Alaska in a matrix population model to estimate the trend and strength of the recovery across this region between 2003 and 2013. A primary impetus for this work was to determine if these vital rates are representative of the current population trend. The population trend was also subjected to prospective and retrospective life history response experiments to determine future trends and which vital rates pose the greatest threats to recovery. The modeled population grew at a mean rate of 4.1% per yr between 2003 and 2013 and was correlated with census count data from the local rookery and throughout the eastern Gulf of Alaska. If density independent growth is to be expected, the eastern Gulf of Alaska population may be fully recovered to pre-decline levels within 14 years. With density dependent growth, the population will need another 37 years to fully recover. As expected, population growth rate had the greatest sensitivity to adult survival, less sensitivity to variation in juvenile survival, and least sensitivity to fecundity. These results have important implications

for population management and suggest current research priorities should be shifted to a greater emphasis on survival rates and causes of mortality.

## INTRODUCTION

Long-term studies of vital rates among wild animal populations are invaluable for understanding population dynamics (Clutton-Brock and Sheldon 2010), and changes in population trends can be well explained by life-history modeling (Sæther et al. 2013). Leslie (1945, 1948) laid the groundwork for modeling population dynamics with matrices based on age-structure and vital rates. Variations of this theoretical work are now widely used to understand aspects of declining, stable, and increasing populations of wild animals (Taylor and Carley 1988).

Population ecology was further developed with theories of life history evolution that focused on *r*- and *K*-selection (MacArthur and Wilson 1967; Pianka 1970), with *r*-selected species generally characterized as short lived and rapidly growing with high reproductive rates, and *K*-selected species exhibiting slow growth, long life, and generally low reproductive output. Later theories spurned *r-K* selection and shifted to a focus on demographic modeling with density-independent, age-specific mortality used to explain life-history evolution, and species described on a fast to slow continuum of lifestyles (Stearns 1983, 1992). However, many aspects of *r-K* selection theory remain valid and useful for characterizing population growth and density-dependent regulation (Reznick et al. 2002).

Steller sea lions (*Eumetopias jubatus*) are grouped among the pinnipeds, which can be considered *K*-selected, or at the slow end of the life-history continuum (Stearns 1983). They give birth to one offspring per year, but not necessarily every year, they have long lactation

periods (9 mo to 4 yrs), and they do not reach sexual maturity until 4.5 yrs of age on average (Pitcher and Calkins 1981; Trites et al. 2006). Steller sea lions experienced a sharp decline in numbers between the 1970s and the 1990s (Loughlin 1998), prompting the 1997 listing of the western distinct population segment (WDPS) as endangered under the Endangered Species Act of the United States (Federal Register 62:30772-30773). The declines were primarily attributed to decreased juvenile survival, an increase in mean adult female age, and a slight decrease in reproductive rates (York 1994). Leading hypotheses for those vital-rate changes include predation by killer whales (*Orcinus orca*), reductions in the availability of important prey items, or a combination of those factors in addition to conflicts with commercial fisheries (Atkinson 2008a; Loughlin and Nelson 1986; National Research Council 2003), whereas contaminants and disease factors are not thought to have greatly affected their vital rates (Burek et al. 2005; Myers et al. 2008; National Research Council 2003). By the early 2000s, much of the WDPS had stopped declining, and numbers have begun to increase in some areas (Eberhardt et al. 2005; Fritz et al. 2013). The upswing in numbers may be attributed to improved juvenile survival and high reproductive rates (Maniscalco 2014; Maniscalco et al. 2014; Chapters 2 and 3). However, given their relative position at the slow end of the life-history continuum, recovery of pinniped populations can take decades (Gerber and Hilborn 2001; Lotze et al. 2011).

The purpose of this study was to apply current mark-recapture-based vital rate estimates of Steller sea lions to a matrix population model to assess the rate of the population recovery in the eastern Gulf of Alaska (EGOA). This work compares the modeled population trends with census counts over the years 2003 – 2013 and forecasts future trends based on both density dependent and density independent models. Additionally, a life table response experiment

(Caswell 1989) is presented to determine the greatest demographic threats to population recovery.

Substantial variation in vital rates can be expected with natural environmental variation and climate change (Boyce et al. 2006; McMahon and Burton 2005; Sæther et al. 2013; Sandvik et al. 2012). Environmental perturbations may cause changes in life history traits that covary positively with each other; e.g., a reduction in food supply may inhibit both fecundity and survival rates (Sæther et al. 2013). Yet, vital rates that have the greatest influence on population trends tend to be more stable, as explained by the demographic buffering hypothesis (Gaillard et al. 2000; Pfister 1998). Among long-lived marine animals, stability in adult survival generally buffers against greater temporal variance in fecundity and juvenile survival (Rotella et al. 2012; Sandvik et al. 2012). Steller sea lions may have an additional buffering mechanism brought about by vital rates that covary negatively. That is, mature females that skip or abort a pregnancy in one year, tend to nurse their dependent offspring for an additional year (Pitcher and Calkins 1981). Such behavior greatly increases survival probability of juveniles between 1 and 2 yrs of age (Maniscalco 2014; Chapter 2). Therefore, reductions in fecundity can be offset to some degree by an increase in juvenile survival. In this manner, Steller sea lion populations may continue to increase even during periods of reduced reproduction.

## MATERIALS AND METHODS

### *Ethics Statement*

This research was conducted in accordance with Alaska SeaLife Center Institutional Animal Care and Use Committee Protocol No. R10-03-01 and National Marine Fisheries Service Permit No. 14324 for research on endangered Steller sea lions. The Chiswell Island

group is part of the U.S. Fish and Wildlife Service Alaska Maritime National Wildlife Refuge. Research was conducted on refuge lands under Right-of-Way Permit No. M-344-AM and Special Use Permit No. 74500-10-001 and earlier versions.

*Study Site and Methods*

The focal area of this study was the Steller sea lion rookery on Chiswell Island in the EGOA, part of the endangered WDPS (Figure 4.1), over the years 2003 to 2013. The population decline at the Chiswell rookery was similar to that of other rookeries throughout the broader Gulf of Alaska (GOA), where abundance fell by 90% from 1,106 adults in 1976 (Calkins et al. 1994) to approximately 90 adults and 50-80 pups in the 2000s (Maniscalco et al. 2006).

Steller sea lions were monitored from at least 6:00 AM to 10:00 PM using 4 to 6 remotely operated video cameras placed on the island (see Maniscalco et al. 2006 for details). Complete census counts of all Steller sea lions by age class (adult males, adult females, juveniles 1 – 4 yrs old, and pups 0 – 1 yrs old) on the rookery were conducted at approximately 11:00 AM and 7:00 PM between 20 June and 10 July during all years of the study. This date range corresponds to range-wide flight surveys for population counts conducted by the National Marine Fisheries Service (Fritz et al. 2008, 2013), thus allowing comparisons with broader regional data and modeled population trends.

Fecundity (also referred to as natality) and survival rates, previously estimated for this rookery (Maniscalco 2014; Maniscalco et al. 2014; Chapters 2 and 3), were used as input data to a life table matrix generally following recommendations by Taylor and Carley (1988) (Table 4.1). The starting population was based on pup and non-pup population counts at rookeries and haulouts in the EGOA between 2000 and 2002 by the National Marine Fisheries Service

(DeMaster 2009, 2011), with non-pup numbers following a Weibull distribution (Weibull 1951). The total population of age 1+ Steller sea lions for each subsequent year (2003 – 2013) was defined as:

$$N_t = \left( \sum_{i=1}^{n} N_{x,t-1}^{f} \cdot p_{x,t} \right) + \left( \sum_{i=1}^{n} N_{x,t-1}^{m} \cdot q_{x,t} \right) \qquad \text{(Equation 4.1)}$$

where $N_{x,t-1}^{f}$ and $N_{x,t-1}^{m}$ are the female and male proportions of the population, respectively. Survival probabilities for females ($p_{x,t}$) and males ($q_{x,t}$) were specific to age ($x$) but not specific to year ($t$) except for first year survival as follows (Table 4.1). First year survival was modeled identically for males and females (Maniscalco 2014; Chapter 2) as the product of neonatal survival for each year (Maniscalco et al. 2008), and a year-invariant survival from approximately 3 weeks to 1 year of age (80.1%; Maniscalco 2014; Chapter 2). Juvenile survival from ages 1 to 4 was specific to age and sex ($p_x^j$ and $q_x^j$ for females and males respectively), but did not vary across years (Maniscalco 2014; Chapter 2). Adult female survival ($p_x^a$, ages 5+) also did not vary across years and was modeled using a Weibull distribution (Weibull 1951; York 1994) with a peak at 8 yrs of age and an overall average of 88.1% (Maniscalco et al. 2014; Chapter 3). Subadult and adult male survival estimates are currently unavailable for the EGOA. Therefore, survival of males at ages 5+ ($q_x^a$) was modeled as 90% of the female survival estimates. This adjustment is based on similar differences in survival between Steller sea lion sexes in the eastern distinct population segment (Hastings et al. 2011).

The number of new pups joining the population each year was assumed to be equal between the sexes and defined as:

$$m_t = F_t \cdot N_t^F \qquad \text{(Equation 4.2)}$$

with $N_t^F$ being the number of mature females (age 5+) in year $t$, and $F_t$ being the fecundity (natality rate) of adult females specific to years 2003 – 2012 (Maniscalco et al. 2014; Chapter 3) and based on this 10-yr average for 2013 and future projections.

Population estimates from the life table were subsequently validated by testing for a correlation with maximum census counts from the Chiswell Island rookery and with counts from the broader EGOA region across the study period.

The population trend for the EGOA was then projected into the future using the logistic growth equation, assuming a stable age distribution (Verhulst 1845):

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right) \qquad \text{(Equation 4.3)}$$

where the intrinsic maximum rate of increase ($r$) over the study period was defined by the dominant eigenvalue of $\lambda$ (asymptotic population growth rate) with $r = \ln \lambda$ (Caswell 1989). This projection assumed a carrying capacity ($K$) of 10,000 Steller sea lions, which is roughly similar to population estimates in the EGOA during the late 1970s when Steller sea lion abundance was at a peak in this region (Calkins et al. 1994).

Population model projections were subjected to retrospective and prospective sensitivity analyses (Caswell 1989, 2000) by varying the vital rate estimates described above to ascertain the greatest potential detriments to population recovery. Ideally, these rates should be covaried based on their relative correlations to each other (Doak et al. 2005; Gaillard et al. 2000). However, juvenile and adult survival did not vary significantly across the study period (Maniscalco 2014; Maniscalco et al. 2014; Chapters 2 and 3) and there was no correlation between fecundity and first-year (pup) survival. Therefore, vital rates were scaled in a retrospective analysis based on the observed stochastic variation in fecundity and first year survival over the 10-yr period 2003 – 2012 (Table 4.1). Random selections (n = 500) were made

from the 10 values of fecundity and first year survival and applied to life history matrices to obtain bootstrapped estimates of the population trend with 95% confidence intervals. This analysis was conducted without density dependence because some recovering pinniped populations go through an extended period of density independent growth (Bowen et al. 2003), and it was of interest to determine the earliest predictable time to full recovery of the Steller sea lion population.

Vital rates were also varied systematically in a prospective analysis to determine the greatest threats to population recovery under multiple scenarios as follows: fecundity was scaled between 0.8 and 1.1 times the rates used in the life table, while adult survival was scaled between 0.8 and 1.0 times. Adult survival was not scaled >1.0 because survival was very close to 1.0 for females at ages 5 – 10, and a value greater than that would be illogical. Survival for juveniles ages 1 – 4 yrs was also scaled between 0.8 and 1.0 by itself and in combination with changes in both fecundity and adult survival to assess synergistic effects of covarying vital rates. An additional set of scenarios tested for an effect of negative covariation between fecundity and juvenile survival by increasing survival to age 2 as fecundity declined. Females that skip a year of pupping tend to nurse their previous offspring for an additional year, thus improving its chances of survival. Therefore, as fecundity declined, survival of female offspring to age 2 was increased from 0.642 to 0.882 based on survival estimates for females weaned at age 1 and those not weaned until age 2 (Maniscalco 2014; Chapter 2). This allowed for modest, but realistic, improvements in juvenile survival that can offset a reduction in fecundity in this species.

## RESULTS

Using current vital rates (Table 4.1) in a life table matrix, the reconstructed Steller sea lion population increased yearly over the study period. This trend held true for pups, mature females, and total age 1+ animals, although juvenile numbers were somewhat irregular due to variation in first year survival across the study period (Table 4.2). Growth in the reconstructed population resulted in a decrease in the mean age of 3 yrs and older females, from 10.7 yrs in 2003 to 9.6 yrs in 2013. The population did not converge on a stable age distribution during this time period, but would be expected to do so within the next 10 to 15 yrs, if vital rates do not change significantly in the near future.

The reconstructed population of age 1+ Steller sea lions increased at a mean rate of 4.1% per year (Figure 4.2). These population estimates were correlated with census counts of the breeding and juvenile population at Chiswell Island between 2003 and 2013 ($r^2 = 0.748$, $P = 0.001$), and at index sites throughout the entire EGOA between 2004 and 2011 ($r^2 = 0.724$, $P = 0.015$; Figure 4.2).

The maximum instantaneous rate of increase ($r$) over the study period was 0.062. Considering this rate, and with carrying capacity ($K$) set at 10,000 individuals, the population in the EGOA should reach 90% of $K$ in the year 2052 (95% C.I.: 2046 – 2061; Figure 4.3). However, changes to vital rates can be expected to occur over such a long time period. Therefore, sensitivity of these projections to changes in the vital rates was examined.

Applying a retrospective analysis based on the observed variation in fecundity and first-year survival without regard to density dependence resulted in an exponentially increasing population into the future (Figure 4.4). With this scenario, we could expect the EGOA population to reach 10,000 age 1+ animals by 2028 (95% C.I.: 2027 – 2029). By systematically

varying vital rates, we found that fecundity had the least effect on population growth (Figure 4.5). A reduction in fecundity to 80% of current rates (to ~56%) still resulted in an increasing population if juvenile and adult survival remained unchanged (Figure 4.5, top left). Diminishing adult survival had the greatest effect on population projections. With no change in fecundity and juvenile survival, a decline of 10% in adult survival decreased population growth by about 1% per year, and a decline of 20% resulted in a rapid population collapse (Figure 4.5). Juvenile survival had a moderate effect on population projections as numbers still increased by nearly 2% per year with a 10% decline in juvenile survival, provided there is no change in fecundity or adult survival. However, with a 20% decline in juvenile survival, the population decreased by about 1.5% per year (Figure 4.5). Vital rates rarely change independently of each other and therefore, multiple scenarios are presented in Figure 4.5.

Modeling negative covariation between fecundity and juvenile survival results in roughly a 2.7% increase in survival to age 2 with every 10% reduction in fecundity, if the same proportion of females not giving birth continues to suckle their pups for an additional year. Opposing changes in fecundity and second year survival would mean that a reduction in fecundity to 40% of current rates would be required to cause a decline in Steller sea lion populations over the next 25 yrs (Figure 4.6).

## DISCUSSION

Several otariid (sea lions and fur seals) populations have fully recovered from catastrophic collapses over the past 2 centuries (Gerber and Hilborn 2001). The reasons for those population collapses varied from anthropogenic effects of fisheries or directed harvest to natural environmental influences such as El Niño events or disease agents (summarized in

Gerber and Hilborn 2001). Steller sea lions in Alaska may have declined in numbers for a variety of reasons (Atkinson et al. 2008a; Guinette et al. 2006; Loughlin 1998; National Research Council 2003), but regardless of the cause(s), they are now emulating the trends of other otariids in their ability to recover.

The upsurge in numbers is especially strong in the eastern Gulf of Alaska (Fritz et al. 2013) and is fueled by good juvenile survival (Maniscalco 2014; Chapter 2) and good reproductive rates (Maniscalco et al. 2014; Chapter 3). The correlations between the population trend modeled here and census-based population counts suggests that monitoring vital rates at a local level can provide a good indication of broader population dynamics for Steller sea lions. However, the census count data presented in Figure 4.2 also indicate that there may have been a more rapid increase in numbers beginning around 2008; there could be a number of reasons for this apparent upsurge. From a sampling perspective, there can be a degree of uncertainty with population counts conducted once or twice per year, and not in every year, due to process noise and observation error (Knape et al. 2013). Among pinnipeds, uncertainties exist primarily due to process noise, mostly in the form of an unknown proportion of animals being hauled out during the time of census because of a variety of environmental influences (Kastelein and Weltz 1991; Mathews and Pendleton 2006). This proportion likely varies to an unknown extent across any given study period for Steller sea lions and makes estimation of vital rates from census counts difficult or impossible (Maniscalco et al. 2010, 2014; Chapter 3). Estimating vital rates from direct observations at a representative rookery can help verify observed population trends and provide additional insight into vital rates over a larger region. There is also some evidence that the Steller sea lion population surge in the EGOA since 2008 is due, at least in part, to emigration from the central GOA (Fritz et al. 2013). Another possible explanation for the recent

upsurge in numbers is that there may have been a change in first-year survival between the early 2000s and the late 2000s from 55% (Fritz et al. 2014) to 80% (Maniscalco 2014; Chapter 2). Coincidentally, there was a relaxation of killer whale predation on young Steller sea lions at the Chiswell Island rookery after 2004 (Maniscalco et al. 2007; Alaska SeaLife Center unpublished data). A change in first- and second-year survival around 2005 would be reflected in the breeding population at rookeries beginning in 2008, as females become reproductively mature at 4 years of age. Finally, there appears to have been an ecosystem change in 2008 related to the Pacific Decadal Oscillation that stimulated greater production of energy-rich fishes such as capelin (*Mallotus villosus*) in the study area (Hatch 2013). This change could have had minor influences on fecundity and juvenile survival, although no change was detected in Steller sea lion vital rates over the 2003 – 2013 study period (Maniscalco 2014; Maniscalco et al. 2014; Chapters 2 and 3).

Regardless of the ultimate cause(s), the rapid increase of Steller sea lion numbers in the EGOA suggests that there is little density-dependent control on the population trend at present. If current trends and density independence are to be expected into the near future, this region of the WDPS may soon enter an exponential growth phase and recover to peak numbers within 13 to 15 years (Figure 4.4). Should density dependent factors come into play, the recovery may take more than twice as long according to population models presented here. The current rate of increase is similar to that seen in other pinniped populations recovering from drastic declines, such as northern elephant seals (*Mirounga angustirostris*; Stewart et al. 1994), gray seals (*Halichoerus grypus*; Bowen et al. 2003), South American sea lions (*Otaria flavescens*; Dans et al. 2004), and New Zealand fur seals (*Arctocephalus forsteri*; Gales et al. 2000). Those populations have been increasing by 4 – 13% per year in recent decades and some have

experienced an exponential growth phase (Bowen et al. 2003), similar to what we may now, or may soon be, observing with Steller sea lions in the EGOA.

Projecting the population into the future, we found that the trends were least sensitive to variation in fecundity and most sensitive to variation in adult survival as would be expected for a long-lived *K*-selected species (Oli and Dobson 2003). In mammals that have delayed maturity and low reproductive rates, survival is much more influential on population growth than fecundity (Crone 2001; Oli and Dobson 2003). Population growth in the presence of environmental stochasticity is buffered in long-lived mammals by stability in adult survival, followed by juvenile survival and fecundity (Gaillard et al. 2000; Sæther et al. 2013). Among pinnipeds, this type of demographic buffering, as evidenced here in Steller sea lions, has also been found in Weddell seals (*Leptonychotes weddelli*; Rotella et al. 2012).

It is suggested here that Steller sea lions may have an additional buffering mechanism in which a reduction in fecundity could result in an increase in juvenile survival (Maniscalco 2014; Chapter 2). Such negatively varying vital rates are usually observed as a cost of reproduction (Bell 1980), where females that reproduce often have reduced chances of survival. Depending on environmental conditions and life history characteristics, females may also forego their own fitness in favor of enhancing the survival likelihood of their offspring (Lindstrom 1999). However, in many cases vital rates will vary in the same direction (Rotella et al. 2012; Sandvik et al. 2012), as they apparently did for Steller sea lions during the period of the decline when fecundity declined along with juvenile survival (York 1994). Whether these vital rates covary negatively or positively will depend on the source of environmental pressures (Gaillard et al. 1998; Reznick et al. 2002). In Steller sea lions, a modest reduction in food availability or increase in disease could negatively affect reproduction (Pitcher et al. 1998), but juveniles that

continue to suckle for an additional year will benefit from their mothers skipping a year of reproduction (Maniscalco 2014; Chapter 2). On the other hand, killer whale predation (Springer et al. 2003; Williams et al. 2004) or anthropogenic effects (Atkinson et al. 2008a; Fritz et al. 1995) may affect survival of all age classes. This suggests that the major declines in Steller sea lion numbers between the 1970s and 2000 may have been multifactorial, but driven primarily by predation and/or direct effects of commercial fisheries (shooting and entanglement), because a drastic population decline in Steller sea lions cannot be explained by moderate reductions in fecundity. Yet, a moderate decrease in juvenile survival along with a modest decline in adult survival can cause a population crash as modeled here.

An estimated 20,000 Steller sea lions were killed by direct interactions with the fishing industry (primarily shooting and net entanglements) between 1968 and 1985, and most were females (Fritz et al. 1995; Loughlin and Nelson 1986). Fisheries restrictions around major rookeries apparently had a mitigating effect on the population decline (Hennen 2006), but those losses alone cannot explain the population crash. Additionally, a small number of killer whales focusing their predation on Steller sea lions could effectively collapse the population (Williams et al. 2004). These are factors that can most certainly cause rapid and deep population declines, whereas evidence of effects of diet on the health and survival of juvenile and adult sea lions is sparse and highly equivocal (Atkinson et al. 2008b; Calkins et al. 2013; Fritz and Hinckley 2005). The effect of diet on fecundity is currently unknown for Steller sea lions, but a change in the population trend is unlikely unless fecundity dropped by more than 50%, and there is no evidence for that (Maniscalco et al. 2010, 2014; Chapter 3).

The recovery of the western population of Steller sea lions is well underway, but looking to the future, we can expect the greatest threats will be factors that have an effect on survival of

adults and juveniles. Minor changes in diet are unlikely to have substantial impacts on adult and juvenile survival, as Steller sea lions are adaptable to a varied diet (Atkinson et al. 2008a; Calkins et al. 2013). Mortality based on conflicts with fisheries has been mitigated due to laws, fishing restrictions, and greater awareness and, therefore, are not expected to be a future threat (Atkinson et al. 2008a). Predation on Steller sea lions by killer whales, and also by sleeper sharks (*Somniosus pacificus*), does remain as a potential threat to recovery (Horning and Mellish 2012, 2014; Williams et al. 2004) and should continue to be monitored. Changes in the population trend of Steller sea lions can be detected by monitoring vital rates at a representative rookery using a variety of mark-recapture statistics. Furthermore, specific threats to the population can be better pinpointed with such detailed monitoring in contrast to census counts alone. The Chiswell Island remote video monitoring project (Maniscalco et al. 2006, 2010) is an excellent study site for continued monitoring of Steller sea lion vital rates and a variety of other behavioral and population-based research objectives.

## ACKNOWLEDGMENTS

Data collection for this study was accomplished by many hard-working technicians and interns at the Alaska SeaLife Center including Juliana Kim, Carlene Miller, Emily Teate, and many others. We thank them and Tuula Hollmen, Lara Horstmann, Sara Iverson, Chuck Frost, and Jason Waite for discussions, commentaries, and much helpful advice on this material.

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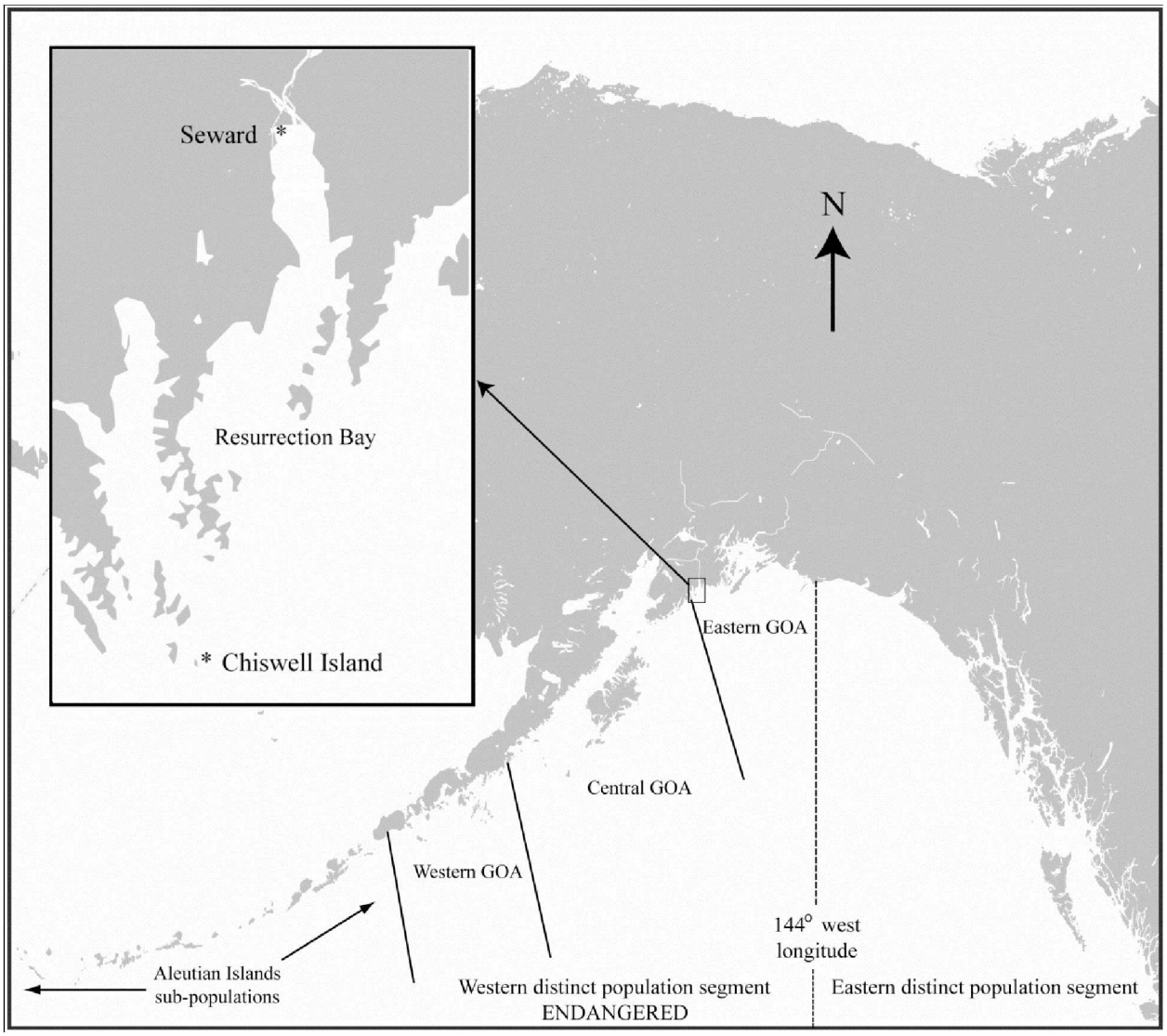


Figure 4.1 – Map of the study area (inset) in the eastern Gulf of Alaska (GOA). The division of Steller sea lion populations into the eastern and western distinct population segments at 144° west longitude, as well as other subpopulations as noted.

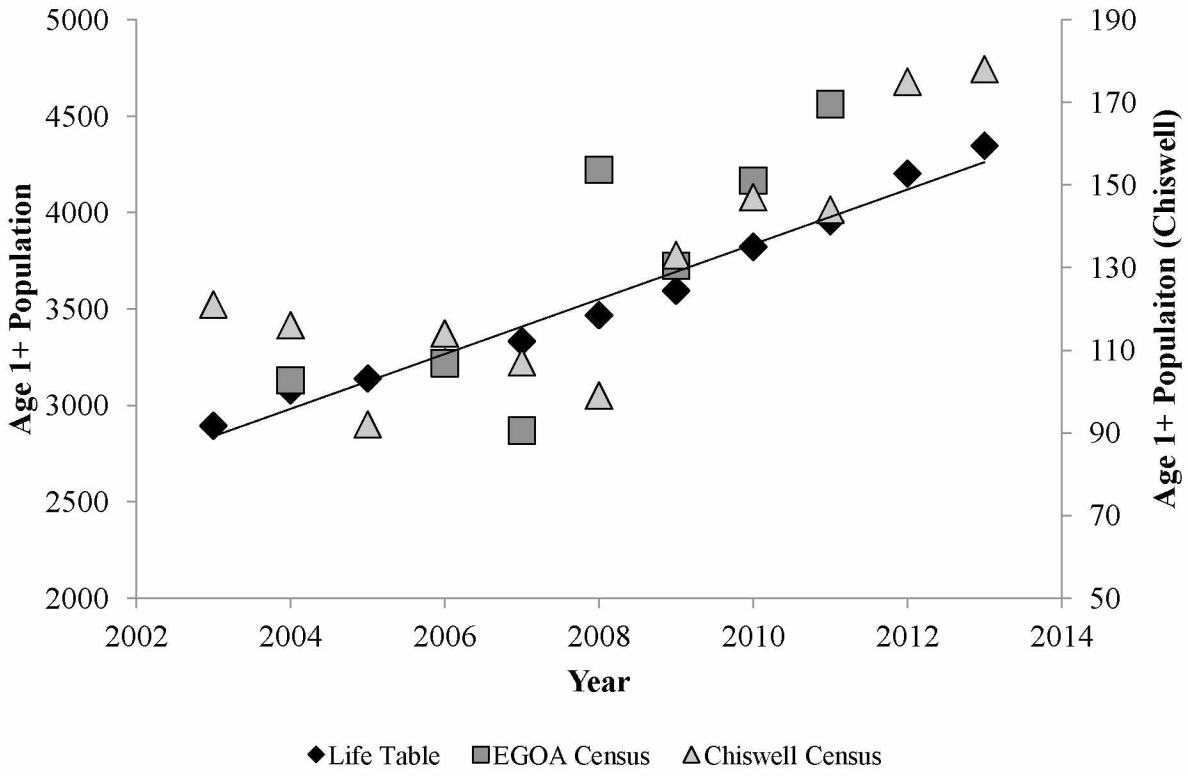


Figure 4.2 – Population trend for Steller sea lions estimated from life tables (Table 4.2; black diamonds and trend line: $r^2 = 0.977$, $P < 0.001$), census counts across the eastern Gulf of Alaska (DeMaster 2011; dark gray squares), and Chiswell Island census counts (gray triangles).

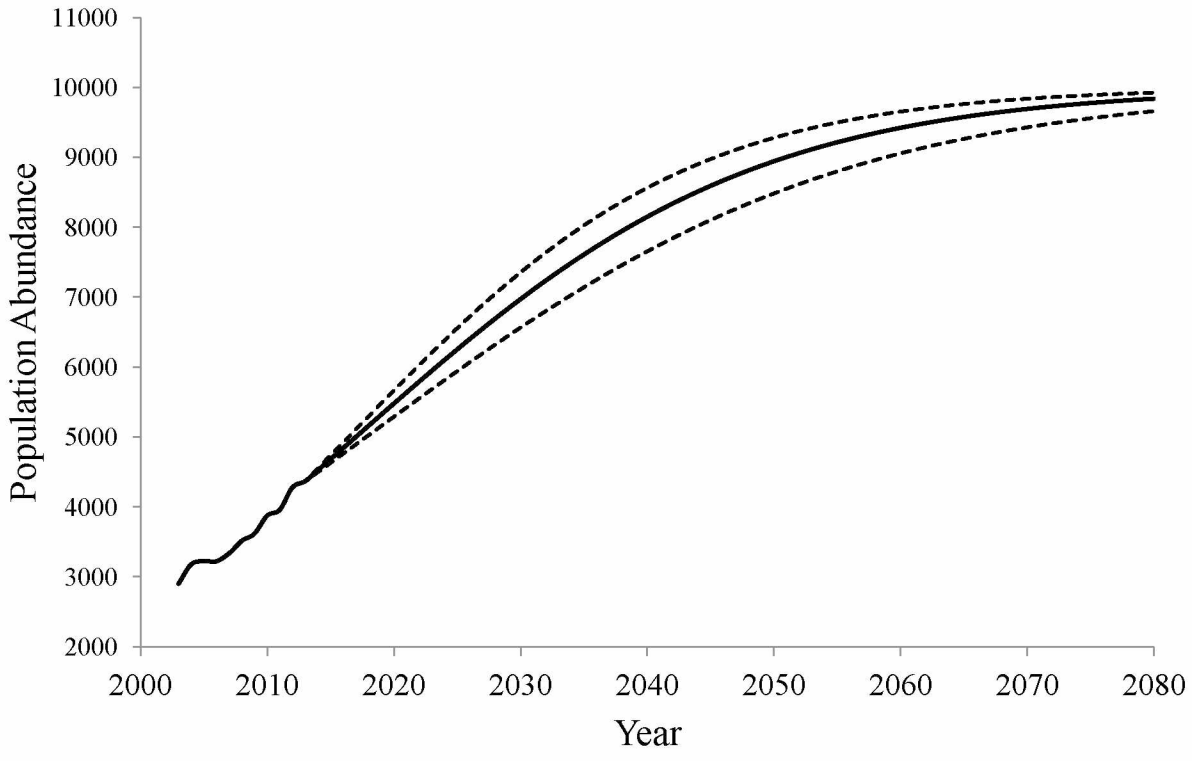


Figure 4.3 – Projected population trend (solid line) ± 95% C.I. (dashed lines) for Steller sea lions in the eastern Gulf of Alaska based on an intrinsic rate of increase of $r = 0.062$ and carrying capacity of $K = 10{,}000$ age 1+ males and females.

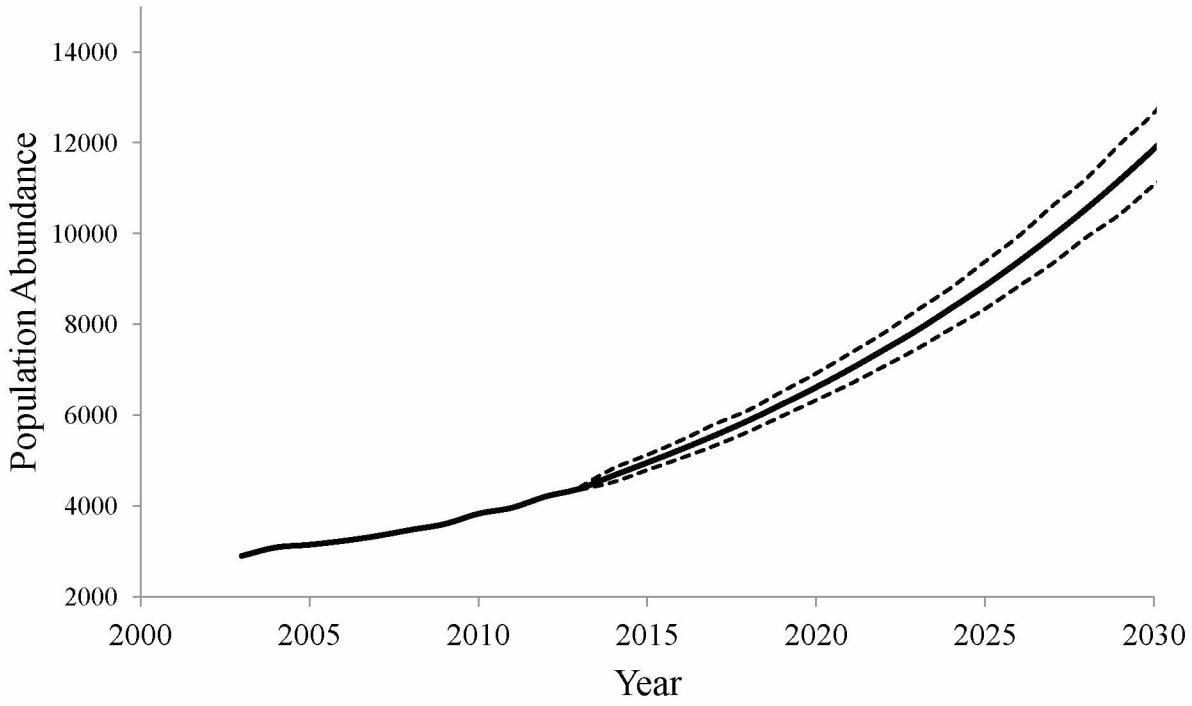


Figure 4.4 – Density-independent projections (solid line) ± 95% C.I. (dashed lines) of the Steller sea lion population in the eastern Gulf of Alaska based on bootstrapped values of fecundity and first-year survival observed over the years 2003 – 2012.

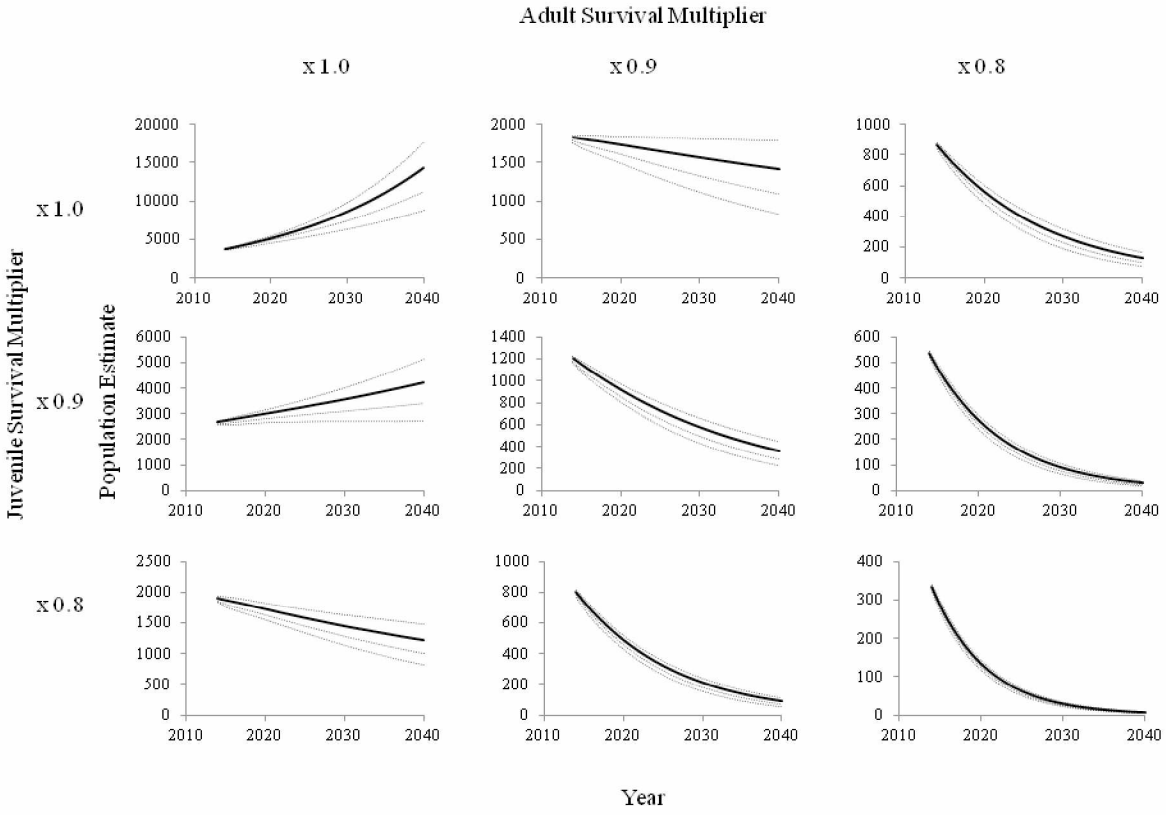


Figure 4.5 – Population projections based on multiple changes in vital rates. Left to right represents reductions in adult survival from 1.0 to 0.8, whereas top to bottom represents reductions in juvenile survival from 1.0 to 0.8 from current estimates. The dark line within each graph represents no change in current rates of fecundity, whereas the upper and lower 2 dotted lines represent change in fecundity to 1.1, 0.9, and 0.8 in decreasing fashion.

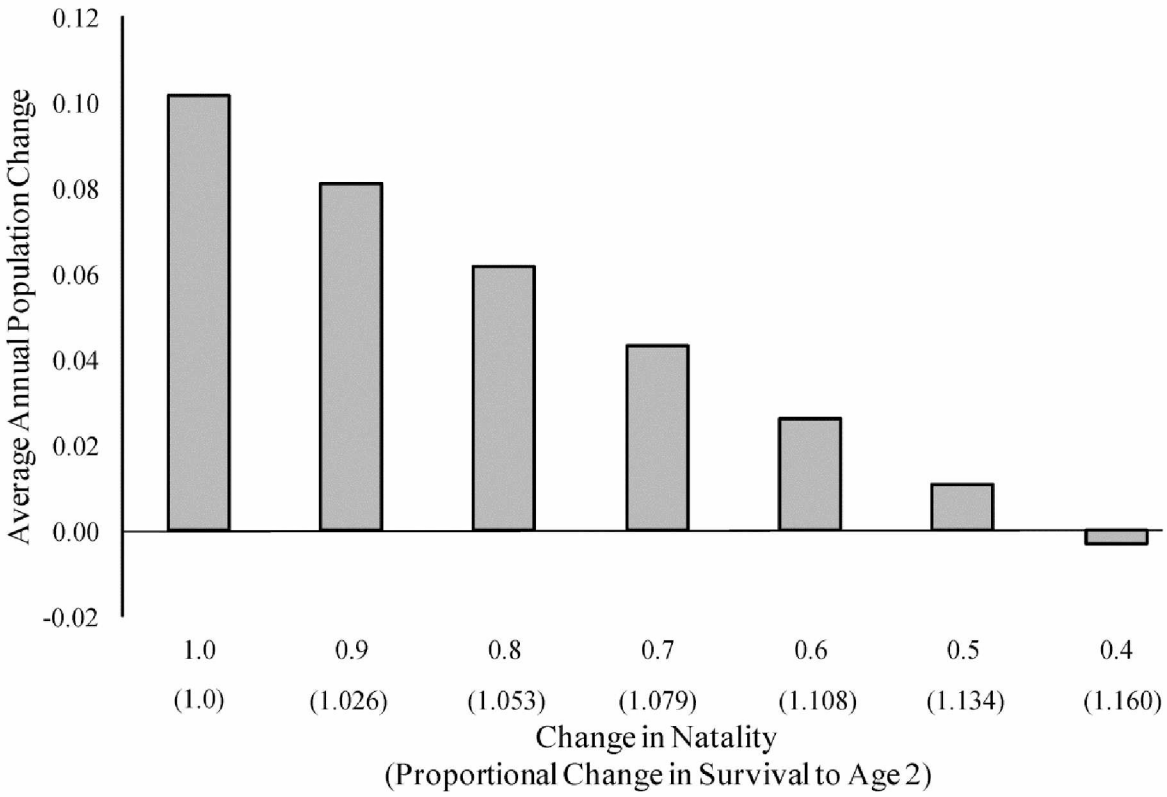


Figure 4.6 – Expected population change (y-axis) if survival to age 2 increases proportional to decreasing fecundity as females that skip a year of giving birth continue to suckle their yearlings. The x-axis represents the change in natality from current estimates and the proportional change in juvenile survival in parentheses.

Table 4.1 – Fecundity and survival parameters used in the life table calculations of Steller sea lion population estimates in the eastern Gulf of Alaska. Fecundity and age 1 survival were specific to year, while survival to age 2+ varied between the sexes but was the same across years based on published data (Maniscalco 2014; Maniscalco et al. 2014; Chapters 2 and 3) and a Weibull distribution on age.

| Year | 2003 | 2004 | 2005 | 2006 | 2007 | 2008 | 2009 | 2010 | 2011 | 2012 | 2013 |
|---|---|---|---|---|---|---|---|---|---|---|---|
| **Fecundity** | 0.745 | 0.718 | 0.676 | 0.697 | 0.718 | 0.698 | 0.708 | 0.689 | 0.721 | 0.693 | 0.707 |
| **Age1 survival** | 0.733 | 0.771 | 0.712 | 0.736 | 0.721 | 0.717 | 0.710 | 0.765 | 0.705 | 0.729 | 0.678 |
| **Survive to age** | Female | Male | | | | | | | | | |
| **2** | 0.695 | 0.406 | | | | | | | | | |
| **3** | 0.923 | 0.828 | | | | | | | | | |
| **4** | 0.942 | 0.805 | | | | | | | | | |
| **5** | 0.962 | 0.866 | | | | | | | | | |
| **6** | 0.974 | 0.877 | | | | | | | | | |
| **7** | 0.980 | 0.882 | | | | | | | | | |
| **8** | 0.983 | 0.884 | | | | | | | | | |
| **9** | 0.982 | 0.883 | | | | | | | | | |
| **10** | 0.978 | 0.880 | | | | | | | | | |
| **11** | 0.972 | 0.875 | | | | | | | | | |
| **12** | 0.964 | 0.868 | | | | | | | | | |
| **13** | 0.955 | 0.860 | | | | | | | | | |
| **14** | 0.945 | 0.850 | | | | | | | | | |
| **15** | 0.933 | 0.840 | | | | | | | | | |
| **16** | 0.921 | 0.829 | | | | | | | | | |
| **17** | 0.908 | 0.817 | | | | | | | | | |
| **18** | 0.894 | 0.805 | | | | | | | | | |
| **19** | 0.880 | 0.792 | | | | | | | | | |
| **20** | 0.866 | 0.779 | | | | | | | | | |
| **21** | 0.851 | 0.766 | | | | | | | | | |
| **22** | 0.836 | 0.752 | | | | | | | | | |
| **23** | 0.820 | 0.738 | | | | | | | | | |
| **24** | 0.805 | 0.724 | | | | | | | | | |
| **25** | 0.789 | 0.710 | | | | | | | | | |
| **26** | 0.773 | 0.696 | | | | | | | | | |
| **27** | 0.757 | 0.682 | | | | | | | | | |
| **28** | 0.742 | 0.668 | | | | | | | | | |
| **29** | 0.726 | 0.653 | | | | | | | | | |
| **30** | 0.710 | 0.639 | | | | | | | | | |

Table 4.2 – Life table population estimates for females and the total age 1+ male and female population (see also, Figure 4.2).

| Age | 2003 | 2004 | 2005 | 2006 | 2007 | 2008 | 2009 | 2010 | 2011 | 2012 | 2013 |
|---|---|---|---|---|---|---|---|---|---|---|---|
| **Age0 (pups)** | 401.6 | 404.7 | 397.9 | 426.8 | 456.8 | 460.3 | 501.3 | 516.1 | 570.2 | 578.9 | 624.1 |
| **1** | 220.0 | 309.6 | 288.2 | 293.0 | 307.7 | 327.4 | 326.7 | 383.3 | 363.9 | 415.7 | 392.7 |
| **2** | 152.9 | 152.9 | 215.2 | 200.3 | 203.7 | 213.9 | 227.5 | 227.1 | 266.4 | 253.0 | 289.0 |
| **3** | 141.2 | 141.2 | 141.2 | 198.7 | 184.9 | 188.0 | 197.4 | 210.1 | 209.7 | 246.0 | 233.5 |
| **4** | 133.0 | 133.0 | 133.0 | 133.0 | 187.2 | 174.2 | 177.1 | 186.0 | 197.9 | 197.5 | 231.7 |
| **5** | 128.0 | 128.0 | 128.0 | 128.0 | 128.0 | 180.1 | 167.6 | 170.5 | 179.0 | 190.4 | 190.1 |
| **6** | 75.7 | 124.7 | 124.7 | 124.7 | 124.7 | 124.7 | 175.4 | 163.3 | 166.0 | 174.3 | 185.5 |
| **7** | 74.2 | 74.2 | 122.2 | 122.2 | 122.2 | 122.2 | 122.2 | 172.0 | 160.1 | 162.8 | 170.9 |
| **8** | 72.9 | 72.9 | 72.9 | 120.1 | 120.1 | 120.1 | 120.1 | 120.1 | 169.0 | 157.3 | 160.0 |
| **9** | 71.6 | 71.6 | 71.6 | 71.6 | 117.9 | 117.9 | 117.9 | 117.9 | 117.9 | 165.9 | 154.4 |
| **10** | 70.0 | 70.0 | 70.0 | 70.0 | 70.0 | 115.3 | 115.3 | 115.3 | 115.3 | 115.3 | 162.2 |
| **11** | 68.0 | 68.0 | 68.0 | 68.0 | 68.0 | 68.0 | 112.0 | 112.0 | 112.0 | 112.0 | 112.0 |
| **12** | 65.6 | 65.6 | 65.6 | 65.6 | 65.6 | 65.6 | 65.6 | 108.0 | 108.0 | 108.0 | 108.0 |
| **13** | 62.6 | 62.6 | 62.6 | 62.6 | 62.6 | 62.6 | 62.6 | 62.6 | 103.2 | 103.2 | 103.2 |
| **14** | 59.2 | 59.2 | 59.2 | 59.2 | 59.2 | 59.2 | 59.2 | 59.2 | 59.2 | 97.5 | 97.5 |
| **15** | 55.2 | 55.2 | 55.2 | 55.2 | 55.2 | 55.2 | 55.2 | 55.2 | 55.2 | 55.2 | 91.0 |
| **16** | 50.9 | 50.9 | 50.9 | 50.9 | 50.9 | 50.9 | 50.9 | 50.9 | 50.9 | 50.9 | 50.9 |
| **17** | 46.2 | 46.2 | 46.2 | 46.2 | 46.2 | 46.2 | 46.2 | 46.2 | 46.2 | 46.2 | 46.2 |
| **18** | 41.3 | 41.3 | 41.3 | 41.3 | 41.3 | 41.3 | 41.3 | 41.3 | 41.3 | 41.3 | 41.3 |
| **19** | 36.4 | 36.4 | 36.4 | 36.4 | 36.4 | 36.4 | 36.4 | 36.4 | 36.4 | 36.4 | 36.4 |
| **20** | 31.5 | 31.5 | 31.5 | 31.5 | 31.5 | 31.5 | 31.5 | 31.5 | 31.5 | 31.5 | 31.5 |
| **21** | 26.8 | 26.8 | 26.8 | 26.8 | 26.8 | 26.8 | 26.8 | 26.8 | 26.8 | 26.8 | 26.8 |
| **22** | 22.4 | 22.4 | 22.4 | 22.4 | 22.4 | 22.4 | 22.4 | 22.4 | 22.4 | 22.4 | 22.4 |
| **23** | 18.4 | 18.4 | 18.4 | 18.4 | 18.4 | 18.4 | 18.4 | 18.4 | 18.4 | 18.4 | 18.4 |
| **24** | 14.8 | 14.8 | 14.8 | 14.8 | 14.8 | 14.8 | 14.8 | 14.8 | 14.8 | 14.8 | 14.8 |
| **25** | 11.6 | 11.6 | 11.6 | 11.6 | 11.6 | 11.6 | 11.6 | 11.6 | 11.6 | 11.6 | 11.6 |
| **26** | 9.0 | 9.0 | 9.0 | 9.0 | 9.0 | 9.0 | 9.0 | 9.0 | 9.0 | 9.0 | 9.0 |
| **27** | 6.8 | 6.8 | 6.8 | 6.8 | 6.8 | 6.8 | 6.8 | 6.8 | 6.8 | 6.8 | 6.8 |
| **28** | 5.1 | 5.1 | 5.1 | 5.1 | 5.1 | 5.1 | 5.1 | 5.1 | 5.1 | 5.1 | 5.1 |
| **29** | 3.7 | 3.7 | 3.7 | 3.7 | 3.7 | 3.7 | 3.7 | 3.7 | 3.7 | 3.7 | 3.7 |
| **30** | 2.6 | 2.6 | 2.6 | 2.6 | 2.6 | 2.6 | 2.6 | 2.6 | 2.6 | 2.6 | 2.6 |
| **Age 1+ F** | **1777** | **1916** | **2005** | **2099** | **2204** | **2322** | **2429** | **2590** | **2710** | **2881** | **3009** |
| **Total Age 1+** | **2893** | **3078** | **3138** | **3223** | **3331** | **3467** | **3594** | **3821** | **3954** | **4201** | **4346** |

# CHAPTER 5

# GENERAL CONCLUSION

Detailed population monitoring at trend-site rookeries and haulouts is considered an essential task to ensure population recovery of endangered Steller sea lions (*Eumetopias jubatus*; National Marine Fishery Service 2008). Chiswell Island can be considered a representative, trend-site rookery in the eastern Gulf of Alaska (EGOA) region of the western distinct population segment (WDPS), because the timing (1970s – 2000) and magnitude (-80%) of the decline at Chiswell Island was the same as observed throughout the Gulf of Alaska (Loughlin 1998; Maniscalco et al. 2010). Likewise, the strength of the recovery at Chiswell Island since the early 2000s is similar to that observed between the eastern Aleutian Islands and the EGOA (close to $4\% \cdot yr^{-1}$; Fritz et al. 2013); a region that is broadly influenced by the Alaska coastal current and input from glacial fjords (Stabeno et al. 2004).

Observational studies of individually marked animals at a representative rookery and overwintering haulouts can be easily accomplished on a year-round basis through the use of a remote video system (Maniscalco et al. 2006, 2010). Long-term studies such as this, illustrate how mechanistic properties of behavior and environment can influence population trends through vital rates, but are somewhat rare because of the continuous funding and research commitment necessary (Clutton-Brock and Sheldon 2010). The Chiswell Island remote video monitoring project (Maniscalco et al. 2006) currently has a 16-year history of tracking individual Steller sea lions that now spans three generations and provides an extensive dataset for detailed research, such as presented in this dissertation.

The principal objectives of this dissertation were to characterize current vital rates of Steller sea lions in the EGOA, primarily juvenile survival (Chapter 2) and female reproductive rates (natality; Chapter 3), and to determine if they are representative of a recovering population (Chapter 4), or if there is still cause for concern. According to these findings, there is currently no reason for concern about vital rates in the study area, but continued monitoring is essential until this species is considered to be fully recovered (National Marine Fisheries Service 2008). The vital rates were also used in a population matrix model to determine the strength of the recovery via retrospective and prospective analyses (Caswell 1989, 2000). Multi-state mark-recapture analyses were conducted in Program MARK (White and Burnham 1999), which allowed estimation of the proportion of juveniles that suckled at different ages and the proportion of females that gave birth in any given year.

Cumulative juvenile survival of Steller sea lions through age 4 was estimated to be 35.7% over the years 2005 – 2012 (Maniscalco 2014; Chapter 2) compared with 17.9% between the late 1980s and early 1990s (Pendleton et al. 2006). Similarly, natality was greater during the past decade (about 70%; Maniscalco et al. 2014; Chapter 3) compared with the height of the population decline in the 1980s (about 55%; Pitcher et al. 1998). The vital rates estimated in this study are consistent with stable and increasing populations of pinnipeds in other regions of the world (Hastings et al. 2011; Lunn et al. 1994; McKenzie et al. 2005). Using matrix population modeling, the rate of increase was estimated at about 4.1% per year during the decade-long study period (Chapter 4). However, an accelerated population increase in the EGOA subsequent to 2008 may indicate either a more recent change in one or more vital rates or immigration of Steller sea lions from other regions (Fritz et al. 2013).

In addition to characterizing current vital rates and population trends, this research revealed new insights regarding demographic buffering and life-history strategies of Steller sea lions. The demographic buffering hypothesis predicts that vital rates that have the greatest effects on population trends (highest elasticity) will be the most stable (Pfister 1998). That hypothesis is generally supported among studies of ungulates (Gaillard et al. 2000), and recently, in Weddell seals (*Leptonychotes weddelli*; Rotella et al. 2012). Similar to findings of those studies, Steller sea lions expressed the least variability and highest elasticity in adult survival, followed by juvenile survival and then reproduction (natality), which had the least elasticity. Furthermore, it appears that Steller sea lions have an additional buffering mechanism by which juvenile survival can be improved. That is, these pinnipeds can offset reductions in natality by continuing to nurse their pups beyond one year of age, and thereby improve offspring survival. Lengthy and variable lactation periods are commonly seen among most otariid pinnipeds (Bonner 1984) and likely evolved in response to unpredictable environmental productivity (Schulz and Bowen 2005). Juveniles that are nutritionally compromised can be more persistent in suckling for an additional year, and thus increase their likelihood of survival, often at the expense of a developing fetus (Trillmich and Wolf 2008). This strategy essentially buffers population losses due to reduced fecundity by improving juvenile survival, which has a higher elasticity and is therefore a greater threat to population recovery compared with fecundity.

Currently, only about 20% of juveniles continue to be nursed beyond age 1 in the EGOA region of the WDPS (Maniscalco 2014; Chapter 2), but I theorize that that proportion would increase during periods of light to moderate food limitation, effectively boosting second-year survival, provided other environmental variables remain constant. With similar variation in lactational dependence (Bonner 1984), it is possible that other otariids have an equivalent life-

history mechanism that may have helped populations to recover from catastrophic collapses (Gerber and Hilborn 2001).

Closely examining the proximate determinants (i.e., vital rates) of population trends as done in this study, can also lead to insights regarding the ultimate reasons for changes in population trends. While it is widely believed that reduced juvenile survival and a moderate reduction in natality were the proximate reasons for the Steller sea lion population decline (Loughlin and York 2000; Pitcher et al. 1998; York 1994), there has been no general agreement as to ultimate cause(s) influencing those vital rates (National Research Council 2003). The three primary theories for ultimate causes are 1) a reduction in preferred prey resources caused by ocean climate changes (Trites et al. 2007), 2) direct and indirect effects of fisheries (Atkinson et al. 2008a; Fritz et al. 1995; Loughlin 1998), and 3) increased predation by killer whales (*Orcinus orca*; Springer et al. 2003; Williams et al. 2004).

Major reductions in food availability have been associated with both reduced survival and reproductive failure among marine mammals, as exemplified by changes during El Niño events for several pinniped species (Melin et al. 2012; Trillmich and Limberger 1985, Trillmich and Ono 1991), and in sea ice habitat loss for polar bears (*Ursus maritimus*; Bromaghin et al. *In Press*). For Steller sea lions, however, general food availability is not believed to have changed greatly over the past several decades in the North Pacific Ocean, although overall quality may have decreased with a greater relative abundance of less fatty fish during the period of decline (Alverson 1992; Anderson and Piatt 1999). These changes in food quality likely do not affect adult survival, and the potential effects on juvenile survival are equivocal (Atkinson et al. 2008b; Calkins et al. 2013). Studies that examine only diet (e.g., Trites et al. 2007) or multiple factors for the population decline (e.g., Guinette et al. 2006; Wolf and Mangel 2008), generally link the

nutritional quality of available prey to Steller sea lion population changes. However, to understand the effects of diet on population trends, we must first understand how a change in diet might affect each vital rate. Then we may be able to link changes in diet to changes in population trends through demographic modeling of the effects on individual vital rates.

Climate change is expected to affect relative food availability for many marine mammals in the Arctic (Bluhm and Gradinger 2008; Kovacs and Lydersen 2008), and some recent studies have observed dietary changes among pinnipeds that were associated with interannual variation in the extent of sea ice (Hindell et al. 2012; Seymour et al. 2014). Determining how vital rates will respond to changes in diet is essential to appropriately ascertain population-level responses, but studies of this nature are challenging to conduct at the individual level where they need to happen (Clutton-Brock and Sheldon 2010). Nevertheless, at least one study did test for a correlation between diet and reproductive status among individual female Pacific walruses (*Odobenus rosmarus*; Seymour 2014). Although no significant correlation was found, more work of this nature is necessary to determine how and if diet variability affects vital rates, and by extension, population trends. It is unknown how or if changes in food quality could affect reproduction in adult female Steller sea lions, but this study has shown that minor or even moderate reductions in natality would not greatly affect population trends (Chapter 4). Yet, the possibility of a dietary effect on female reproduction or juvenile survival deserves more research attention because of the implications.

Given the lack of evidence that a change in diet could produce a substantial change in Steller sea lion population trends, it becomes more likely that the population declines were predominately influenced by other factors, such as anthropogenic effects and/or predation. An estimated 45,000 pups were culled from major rookeries between 1963 and 1972, but those

losses alone cannot explain the severity of the population decline (Pascual and Adkison 1994). In addition, an estimated 20,000 Steller sea lions were killed by direct interactions with the fishing industry between 1968 and 1985 (Fritz et al. 1995; Loughlin and Nelson 1986). Even when taken together, those anthropogenic effects cannot explain a loss of more than 200,000 individuals in the WDPS between the 1960s and 1990s, although they likely had a contributing effect (Atkinson et al. 2008a). Alternatively, it would take only a minor change in the diet of transient killer whales to strongly contribute to the population collapse of Steller sea lions (Williams et al. 2004). Still, there is little direct evidence for changes in killer whale predation, although the theoretical arguments are extensive and well-reasoned (Estes et al. 2009; Springer et al. 2003, 2008). It deserves mention here that killer whales were frequently observed preying on Steller sea lions around the Chiswell Island rookery during the early 2000s (Maniscalco et al. 2007). However, killer whales have rarely been observed at this location since 2005 (ASLC unpublished data), although they may have remained in the broader region feeding on other mammals (Matkin et al. 2012). The greatest Steller sea lion population increases observed in the EGOA were after 2005 (Figure 4.2). Although this evidence for a relaxation in predation pressure by killer whales is circumstantial, it certainly warrants additional study, in addition to the recently recognized threat of predation by sleeper sharks on Steller sea lions (*Somniosus pacificus*; Horning and Mellish 2014).

Much research effort has been dedicated to studying reproduction in Steller sea lions since a theoretical population model suggested continued declines in natality were occurring well into the 2000s (Holmes et al. 2007). The empirical work presented in this dissertation has shown that both natality and juvenile survival in the Gulf of Alaska are strong and indicative of a recovering population. Furthermore, even if natality was somewhat depressed, it would be

unlikely to have had a major negative impact on population trends. This is not being observed at the rookeries that are being monitored (Fritz et al. 2013; Maniscalco et al. 2010, 2014; Chapter 3). On the other hand, given the effect that killer whale predation can have on survival rates of juveniles (Horning and Mellish 2009), dedicated monitoring of population interactions and ecosystem effects are necessary as the WDPS of Steller sea lions continues to recover.

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# APPENDIX 1

## Permission from Co-Author

As co-author on the published manuscript entitled, "A longitudinal study of Steller sea lion natality rates in the Gulf of Alaska with comparisons to census data," I hereby grant my permission for John M. Maniscalco to use this as a chapter in his Ph.D. Dissertation.

12/2/2014

Pamela Parker — Date

# APPENDIX 2

# COPY OF IACUC APPROVAL LETTER

March 23, 2010

Alaska SeaLife Center
windows to the sea

John Maniscalo
Alaska SeaLife Center
P.O. Box 1329
Seward, AK 99664

Dear John:

The following protocol using vertebrate animals was reviewed and approved by the Alaska SeaLife Center Institutional Animal Care and Use Committee (IACUC). The "Assurance of Animal Care" form will be kept on file in the office of the IACUC Recording Secretary.

This Assurance is valid for twelve (12) months after approval and must be kept current with respect to new methods or techniques as they evolve. The Assurance will be returned to you each year for review and, if desired, renewal. It may be renewed for a maximum of two (2) times. Thereafter, a new Assurance must be filed with the IACUC.

All students (undergraduates or graduate) and staff must complete a formal training program in animal care and use. All individuals performing manipulations on vertebrate animals (handling, capture, blood collection, surgery, etc.) must demonstrate proper training, experience, and capability.

If a Letter of Assurance is required by a granting agency, you must notify the IACUC Recording Secretary. It is your responsibility to provide the required contact and agency information prior to the grant deadline.

All vertebrate animal mortality events or events that result in unexpected serious injury to study animals associated with this protocol will be reported to the IACUC within one (1) week of occurrence. Failure to report the event may result in suspension of the protocol.

All vertebrate animals under this Assurance must be identified with the assigned IACUC Protocol number.

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IACUC Protocol Number: R10-03-01 USDA Classification: D

Investigator/Instructor: John Maniscalco

Title of Project/Course: Foraging Ecology of Wild Steller Sea lions

Date Received: Feb 15, 2010

Date Approved: March 23, 2010

Annual renewal: March 2011 and 2012

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APPROVED, as submitted / modified.

Sincerely,

Brett Long, IACUC Chair

Revised 7/24/08